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Editorial

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## EDITORIAL

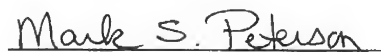
In the early 1960s, Dr. Gordon Gunter, then the Director of Gulf Coast Research Laboratory, almost singlehandedly developed the concept of *Gulf Research Reports* (GRR) as a mechanism "... devoted primarily to publication of the data of the Marine Sciences, chiefly of the Gulf of Mexico and adjacent waters". The first issue appeared in April 1961 and since that time *Gulf Research Reports* has produced 34 issues covering over 280 reports on the resources and processes of the Gulf of Mexico and adjacent waters. Many of the papers in those early issues focused on local and regional issues, processes and problems. Through the years, however, papers appeared from authors outside the local and regional areas which focused on organisms and/or processes relevant to the Gulf of Mexico and adjacent waters. Papers have been published from scientists in Denmark, Germany, Sweden, Canada, Japan, Mexico, and the Caribbean Sea nations, giving a more international flavor to the journal. The Director of the Gulf Coast Research Laboratory (GCRL) served as Editor of GRR until the 1997 issue.

The editorship of GRR was passed on to the late Dr. Harold D. Howse from Dr. Gordon Gunter beginning with the 1975 issue. At that time the journal was reformatted to a larger page size and a nominal page charge was, for the first time, assessed to help defray the cost of publication. The first "Guide to Authors" appeared in that issue and manuscripts had to be found acceptable by at least two referees (Howse, editorial in GRR 5(1)). Dr. Howse was Editor of GRR through 1992 with volume 8(4). Dr. Thomas D. McIlwain became Editor of GRR and guided the 1994 and 1995 issues to print. Interim GCRL Director, Dr. Robert T. van Aller, served as Editor of GRR for the 1996 issue. From 1989 until 1996 Ms. Susan Griggs acted as Assistant or Managing Editor of GRR and provided guidance with her expert editorial and managerial skills.

I formally became Editor-in-Chief of GRR with the 1997 issue and currently serve in that capacity. Changes in GRR procedures instituted in 1997 continue to be modified and refined today. GRR now has an Editorial Board that includes five GCRL scientists who, in association with Managing Editor Linda C. Skupien, provide vital information and guidance for the production of GRR. In 1998, the position of Editorial Associate was added and has been filled by S. Dawne Hard. The Editorial Board is chaired by the Editor-in-Chief. The role of the Editorial Board is to make policy for GRR. All changes and modifications to GRR are discussed, reviewed and voted on by the Editorial Board. A group of Associate Editors was appointed, including the scientists on the Editorial Board, the Editor-in-Chief and national and international experts to bring disciplinary depth and international perspective to GRR. All Associate Editors have a two-year appointment. This major change in GRR policy has

been an important and fruitful one. At this time we removed the page charges for published manuscripts and initiated a nominal subscription fee. The 1997 issue included a complete revision of the "Guide to Authors" and "Scope" of GRR, a change in the volume numbering sequence of GRR issues, and a minor redesign of the cover. The Editorial Board modified the cover again in the 1998 issue by including the new Institute of Marine Sciences logo in lieu of the GCRL logo. Finally, in the 1998 issue (Volume 10), the abstracts from the annual meeting of the Gulf Estuarine Research Society (GERS) were published in GRR. GERS abstracts will continue to appear in GRR. These changes were made to help our readership recognize the changes within the Gulf Coast Research Laboratory, the supporting structure of GRR, (see Preface of Dr. D.J. Grimes in GRR Volume 10).

During 1998, the Editorial Board in consultation with Dr. Grimes began discussions about major changes in GRR. The changes we envisioned will result in the ultimate goal of making GRR a "... widely recognized source of scientific information that underpins the understanding, planning, and management of Gulf of Mexico and Caribbean natural resources and processes" (see Preface of Dr. D.J. Grimes in GRR Volume 10). Our goal was thus to reformulate and repack the original vision of GRR. At the 1998 Editorial Board meeting in December, we voted to again update the "Guide to Authors" and the "Scope" to better reflect our mission and audience. We also voted to remove a published submission deadline such that more manuscripts might be submitted to the journal with the ultimate vision of publishing two issues annually. We voted to change the name of the journal from *Gulf Research Reports* to *Gulf and Caribbean Research*. This change will become effective in Volume 12 published in the year 2000. We feel this name change will more accurately reflect the scope of the papers published in the journal; and we hope our readership will enjoy our new look and name, which we feel will support and extend the original vision of its founder Dr. Gordon Gunter. As this issue was going to press, Dr. Gordon Gunter passed away at the age of 89 on 19 December 1998. The Editorial Board dedicates this issue to his memory and long standing in the Marine Science Community. He will be long remembered as the founder of *Gulf Research Reports*.



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## Recent Trends in Water Clarity of Lake Pontchartrain

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## RECENT TRENDS IN WATER CLARITY OF LAKE PONTCHARTRAIN

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**ABSTRACT** An analysis of Secchi disk transparency observations from 3 sites on the Lake Pontchartrain Causeway indicates that water clarity has increased at the north shore and mid-lake sites, but has not changed at the south shore site. Louisiana Department of Environmental Quality data from 1986 through 1995 were used in the analysis. Further analysis indicates that the increased transparency was not caused by changes in salinity or wind speed. The best explanation for the observed increase is the cessation of shell dredging in 1990.

### INTRODUCTION

Lake Pontchartrain is an estuarine embayment located in southeastern Louisiana, north of metropolitan New Orleans. The lake has a mean salinity of about 4‰, mean depth of 3.7 m and surface area of 1,630 km<sup>2</sup> (Sikora and Kjerfve 1985). Several factors have contributed to the environmental degradation of Lake Pontchartrain including urban and agricultural runoff, shell dredging, saltwater intrusion, operation of the Bonnet Carre Spillway and industrial discharges (Houck et al. 1987). A major environmental concern has been an assumed long-term increase in turbidity based on Secchi disk transparency observations (Stone et al. 1980).

Stone (1980) analyzed 4 sets of Secchi disk transparency data and concluded that water clarity had decreased almost 50% between 1953 and 1978. Francis et al. (1994) also found that regression of the available transparency data on time (1953 through 1990) suggested a statistically significant decrease in transparency of about 40%. The 1953 to 1990 data, however, were biased in that they did not adequately represent the seasonal effects of salinity and wind speed. There are strong correlations between water clarity and salinity and wind speed in Lake Pontchartrain, and both variables vary with season. When the transparency data were adjusted for the seasonal effects of salinity and wind speed or when unbiased data sets were constructed, the data did not support the hypothesis of a change in transparency from 1953 to 1990.

Shell dredging was discontinued during the summer of 1990. It was known to have produced short-term, local increases in turbidity, but may have had more widespread and lasting effects due to the production of unconsolidated bottom sediments that could be more easily resuspended by wind (USACOE 1987). If shell dredging had long-term, widespread effects on water clarity, then a comparison of transparency data from the 1986-90 and 1991-95 periods might reveal an increase in transparency that would be indicative of recovery. Such evidence of recovery would

also suggest that a significant impact from shell dredging had occurred.

The present study was conducted to determine whether changes in water clarity as measured by Secchi disk transparency had occurred since 1990, and thereby provide a sequel to our earlier work (Francis et al. 1994), and also to determine whether any observed changes could be attributed to the cessation of shell dredging in the lake.

### MATERIALS AND METHODS

#### Description of the Data Set

Secchi disk transparency, salinity, and turbidity data for the 1986 to 1995 period were obtained from the Louisiana Department of Environmental Quality (LADEQ). The data were collected as part of an ongoing monitoring program which includes monthly measurements at 3 stations on the Lake Pontchartrain Causeway located approximately 4 miles (6.4 km) from the north shore, at mid-lake, and approximately 4 miles from the south shore (Figure 1). A few data points are missing in the 1986 through 1995 data set because measurements were not taken in some months. The missing data points were estimated by distance weighted least squares.

Wind speed data for the 1986 to 1995 period were recorded daily at the New Orleans International Airport. The data set constructed for this study contains the average wind speed for a 5-day period including the day of transparency measurement and the 4 preceding days.

#### Regional Effects of Wind

Wind probably has the same effect on transparency in all regions of the lake. It is not possible, however, to conduct a rigorous statistical test of that premise with the available data. Multiple regression analysis was used only to provide some support for the idea. Data were selected from the LADEQ data sets for transparency and salinity and from the wind speed data set recorded at the New Orleans International Airport. The combined data set

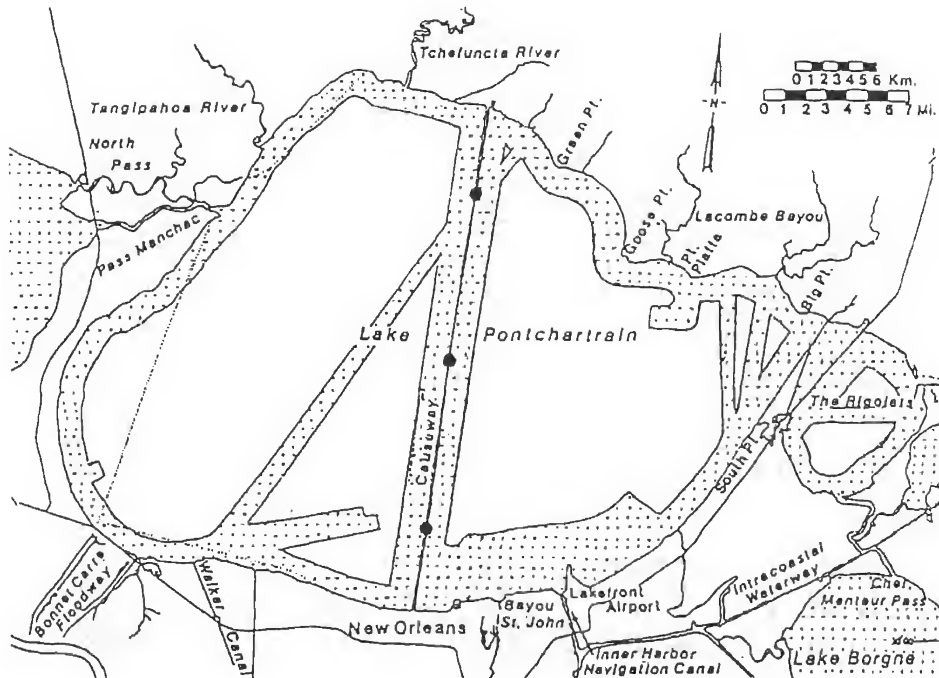


Figure 1. Map of Lake Pontchartrain, Louisiana. The stippled area indicates areas where shell dredging was prohibited (USACOE 1987). The three LADEQ monitoring sites on the Lake Pontchartrain Causeway are indicated by large dots.

has measurements of transparency, salinity and wind speed for 119 months from 1986 through 1995. In 53 months salinity was sufficiently similar at the 3 sampling sites to realize a coefficient of variation of 25 or less. These data were chosen for analysis. The selection procedure was intended to remove salinity as a significant variable in the regression. The selection limit of 25 was an arbitrary choice. There was no autocorrelation in these data.

In regressions of transparency on salinity and wind speed one would expect the partial regression coefficients for salinity not to be significant because of the data selection procedure, and those for wind speed to be significant. If wind speed has the same effect on transparency at the 3 sampling sites, then one would expect 3 parallel regressions with different constants and slopes determined largely by wind. One would expect further that the ratios of constant to slope would be the same if the regressions are parallel.

When transparency was regressed on salinity and wind speed, the partial regression coefficients for salinity were not significant as expected, and those for wind speed were significant at all 3 sites. Ratios of constant to slope were 13.16, 13.51, and 11.40 for the south shore, mid-lake and north shore sampling stations, respectively,

suggesting that a given wind speed produced approximately the same percentage decrease in transparency at the 3 sites, or that wind speed had approximately the same effect in the different regions of the lake.

#### Transparency and Turbidity

Secchi disk transparency measurements were obtained with a 20 cm disk with black and white quadrants. Transparency data were used in the present analysis to facilitate comparison with historic data. Because Secchi disk observations are somewhat subjective, the association between transparency and turbidity data sets was analyzed to corroborate results. Pearson correlation coefficients for transparency and turbidity were greater than 0.8 ( $p < 0.001$ ) for the 3 sampling sites.

#### Statistical Methods

The 4 time-series data sets used in statistical analyses (transparency, turbidity, salinity and wind speed) possess low but statistically significant first order autocorrelation. Autocorrelation was reduced to non-significance in each data set by differencing with one period lag. Each data set thus fits a first order autoregressive model.

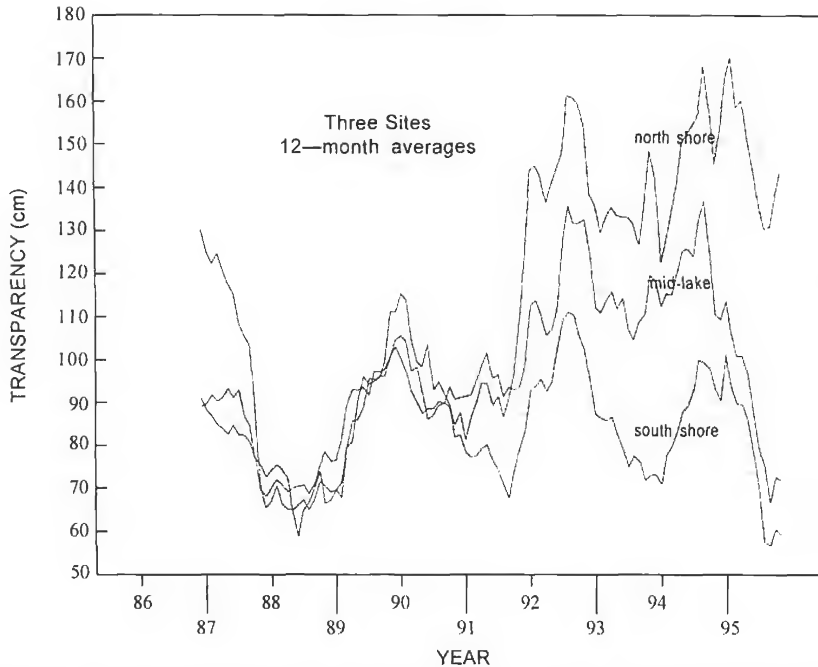


Figure 2. Twelve-month moving averages of monthly Secchi disk transparency at the 3 sampling sites from 1986 through 1995.

Significance tests in analysis of variance and regression analyses were performed with lagged data. Residuals were analyzed to test for normality, homogeneity of variance and independence.

Standardized partial regression coefficients may be obtained with data transformed to standard normal form. Standardized coefficients are useful for comparative purposes because they are independent of scale.

## RESULTS

Twelve-month moving averages of monthly Secchi disk transparency measurements from the south shore, mid-lake and north shore sampling sites are presented in Figure 2. Approximately the same transparency was realized at all 3 sites through 1990. After 1990, transparency increased at the north shore and mid-lake sampling sites, but not at the south shore site. One-way analysis of variance indicated that mean transparencies for the 3 sites in the 1986-90 period were not significantly different,  $p > 0.5$ . In the 1991-95 period, however, mean transparencies for the 3 sites were significantly different from each other,  $p < 0.05$ .

Lake-wide mean salinities were 3.98‰ and 3.17‰ in the 1986-90 and 1991-95 periods, respectively. The 95% confidence intervals for these means overlap, indicating

that the higher transparencies measured in the 1991-95 period were not associated with a significant lake-wide change in salinity. Twelve-month moving averages of monthly salinity measurements from the south shore, mid-lake and north shore sampling sites are presented in Figure 3. Consistently lower salinities occurred at the north shore throughout the 1986-95 period. The 95% confidence interval for north shore mean salinity in the 1991-95 period does not overlap the 95% confidence intervals for mid-lake and south shore mean salinities. The higher transparencies observed at the north shore in the 1991-95 period (Figure 2) were thus associated with salinities lower (Figure 3) than were measured at other regions of the lake.

Lake-wide mean wind speeds were 7.76 mph and 8.13 mph in the 1986-90 and 1991-95 periods, respectively. The 95% confidence intervals for these means overlap, indicating that the higher transparencies measured at the north shore in the 1991-95 period (Figure 2) were not associated with a significant lake-wide change in wind speed.

Multiple regression analysis was used to assess the relative effects of salinity and wind speed on transparency between the 1986-90 and 1991-95 periods for the south shore and north shore sampling sites (Table 1). At the south shore, the partial regression coefficient for salinity

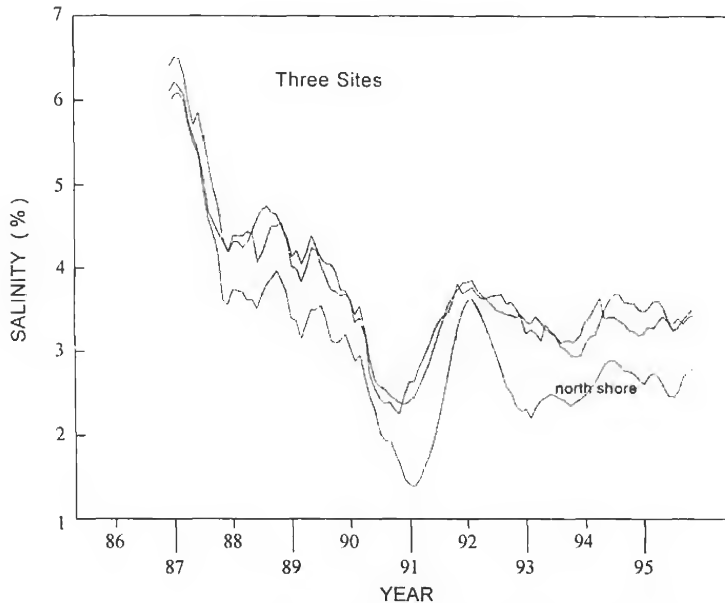


Figure 3. Twelve-month moving averages of monthly salinity at the 3 sampling sites from 1986 through 1995.

was not statistically significant in both periods, suggesting that the negative effect of wind speed was the more prominent factor in determining transparencies. Standardized regression coefficients for salinity at the south shore had overlapping 30% confidence intervals as did standardized coefficients for wind speed. At the north shore, both partial regression coefficients were significant in both periods (Table 1). Standardized regression coefficients for salinity at the north shore had overlapping 30% confidence intervals as did standardized coefficients for wind speed. These results indicate that the relative effects of salinity and wind speed on transparency were different at the 2 sampling sites. More importantly for the purpose of this paper, the results also indicate that the effects of salinity and wind speed were approximately the same in both periods at a given sampling site.

## DISCUSSION

The similarity of standardized regression coefficients in the 1986-90 and 1991-95 periods at the south shore and north shore sampling sites (Table 1) indicate that the higher transparencies measured at the north shore in the 1991-95 period (Figure 2) cannot be explained by changes in salinity or wind speed.

Salinity has a statistically significant positive effect on transparency, and wind speed has a statistically significant negative effect on transparency (Francis et al.

1994). Higher transparencies, therefore, are usually associated with higher salinities and lower wind speeds. An unusual feature of the reported results is that the higher transparencies observed at the north shore in the 1991-95 period were not associated with higher salinities or lower wind speeds, but rather with lower salinities than those measured at the mid-lake and south shore sampling sites and with wind speeds that were the same at the 3 sites.

The higher transparencies (Figure 2) and higher regression constant (Table 1) at the north shore during the 1991-95 period may be explained by the positive effect on transparency realized through cessation of shell dredging. Sediment disruption produced by shell dredging probably had a greater negative effect on transparency in the lower-salinity waters of the north shore (Figure 3) because of the tendency for lower-salinity waters to retain particles in suspension longer (Francis et al. 1994). By reducing transparencies at the north shore in the 1986-90 period, shell dredging probably was responsible for the lower regression constant for that period (Table 1). Shell dredging was not present in the 1991-95 period resulting in higher transparencies and a higher regression constant.

Higher transparency peaks were apparent at the north shore and mid-lake sampling sites by the fall of 1991 (Figure 2). This observation is consistent with expectation because an immediate increase in transparency was not anticipated. Unconsolidated sediments that are more

TABLE 1

Regression analyses of transparency vs. salinity and wind speed for south shore and north shore sites in 1986 through 1990 and 1991 through 1995,

Site and Period	Coefficient	Standardized Coefficient	p
South Shore 1986-90			
Constant	153.57		
Salinity	5.55	0.25	0.213
Wind speed	-11.13	-0.54	0.021
South Shore 1991-95			
Constant	163.84		
Salinity	7.42	0.18	0.389
Wind speed	-13.93	0.61	<0.001
North Shore 1986-90			
Constant	92.11		
Salinity	14.12	0.55	0.006
Wind speed	-6.01	-0.23	0.091
North Shore 1991-95			
Constant	155.63		
Salinity	34.02	0.57	0.003
Wind speed	13.94	-0.37	0.006

susceptible to resuspension by wind (USACOE 1987) would persist for a period of time following dredging and have a longer-term effect on turbidity. In addition, an earlier expression of higher transparency may have been mitigated by lower lake-wide salinities in 1990 and early 1991 (Figure 3) that would have lowered transparency.

Transparency remained essentially unchanged at the south shore after shell dredging was stopped. Several factors may have contributed to this outcome. Dredging was prohibited within 3 miles of the south shore extending from the Lake Pontchartrain Causeway east to Paris Road in Orleans Parish, and near oil and gas facilities in Jefferson Parish west of the causeway (Figure 1). Consequently, dredging and its effects on transparency may have been less intense near the south shore site. The south shore is subject to urban runoff from metropolitan New Orleans, and it has a highly modified shore line with no exchange with natural streams and wetlands. Runoff introduces nutrients that can promote algal growth with the result that turbidity from phytoplankton growth may have replaced turbidity from resuspended sediments.

Shell dredging began in 1933 and probably affected transparency prior to the first transparency measurements in 1953. The cessation of shell dredging in 1990 reestablished conditions favoring higher transparencies in some regions of the lake. The change to higher transparencies cannot be attributed to changes in salinity or wind speed.

#### ACKNOWLEDGMENT

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Effects of Diflubenzuron on the Ontogeny of Phototaxis by *Palaemonetes pugio*

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## EFFECTS OF DIFLUBENZURON ON THE ONTOGENY OF PHOTOTAXIS BY *PALAEMONETES PUGIO*

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**ABSTRACT** The phototaxis by larvae of the grass shrimp *Palaemonetes pugio* that hatched from embryos which were exposed to a single pulse concentration of diflubenzuron (DFB; Dimilin®) was quantified. Stage IV embryos (6-day-old) were exposed to 0.5 µg/L of DFB for 4 days followed by transfer into clean seawater for the rest of the incubation period. The photoresponses of light-adapted larvae from untreated embryos and embryos treated with 0.5 µg/L DFB were monitored from 1 day through 8 day post hatch for phototactic responses to 500 nm light. Larvae from untreated embryos exhibited strong positive phototaxis at high light intensities ( $3 \times 10^{-2}$  and  $3 \times 10^{-1}$  Wm<sup>-2</sup>) but became negatively phototactic at lower light intensities ( $3 \times 10^{-3}$  to  $3 \times 10^{-2}$  Wm<sup>-2</sup>). This phototactic pattern continued during the monitoring period. On the other hand, larvae from DFB-treated embryos exhibited altered phototaxis for the first 3 days. Alterations were especially evident on Day 1, as larvae were only negatively phototactic. By Day 4, these larvae reverted to the normal pattern of photoresponses shown by untreated larvae. These results indicated that the alterations in photoresponses of larvae caused by embryonic exposure to DFB are only transitory and can be corrected within 4 days of hatching if the larvae are exposed to water lacking DFB.

### INTRODUCTION

Diflubenzuron (DFB; Dimilin®) is an insect growth regulator that interferes with chitin formation and molting in arthropods. It is approved for and is being used in the United States for control of a wide variety of insect pests, including foliage feeders on soybeans, cotton-leaf perforator, and forest insects. In California DFB is used to control mosquito larvae (Fischer and Lenwood 1992). The effects of DFB on non-target arthropods, especially aquatic organisms, is well documented (see review by Fischer and Lenwood 1992). There is always the potential for DFB impacting aquatic organisms because of overspray or spills, especially where it is being applied close to water or directly onto wetlands for mosquito control.

Phototaxis and its ecological significance in crustaceans is well documented in the literature (White 1924, Thorson 1964, Forward 1974, Vernberg et al. 1974, Forward et al. 1984, Sulkin 1984). For example, in a review by Thorson (1964) of marine benthic invertebrates, of the 141 species studied, 82% of the early larval stages respond positively to light. Phototaxis has also been reported to play an important role in diel vertical migration of crustacean larvae (Forward 1976, Forward and Cronin 1980, Forward et al. 1984, Forward 1985). Vertical migration contributes to the dispersal of crustacean larvae and helps in their retention in the estuary (Sulkin 1975, Cronin 1979, Cronin and Forward 1986).

For larval stages of estuarine crustaceans, the phototactic pattern, when tested in a narrow light field, is generally negative phototaxis to low light intensities and positive phototaxis to moderate intensities (e.g. Forward

and Costlow 1974). Also, ontogenetic changes in photoresponses are observed in some crustaceans. Generally, the younger stages are more positively phototactic while negative phototaxis increases in the older larval stages, postlarvae, and adults (see review by Pardi and Papi 1961, Dingle 1969). Because of the role of phototaxis in vertical migration of crustacean larvae, any alteration in this photoresponse as a result of exposure to toxicants may affect the ecology and conceivably the larvae's recruitment into the adult population.

Photo behavior has been shown to be very sensitive to changes in environmental factors such as temperature, salinity, and chemicals. Changes in photobehavior have also been used in aquatic toxicology as a sensitive indicator of anthropogenic stress (Rosenthal and Alderdice 1976, Simonet et al. 1978, Lang et al. 1981, Rand 1985). Specifically for larval crustaceans, the following studies have employed changes in photobehavior as indicators of sublethal toxicity: Forward and Costlow (1976) for insect juvenile hormone mimic on *Rhithropanopeus harrisii*; Moyer and Bartholmus (1979) for the herbicide Weeder-64 on *Palaemonetes pugio*; Lang et al. (1980) for copper on *Balanus improvisus*. In all these studies, the larvae were directly exposed to the toxicant followed by measurement of phototaxis. Only Wilson (1985) and Wilson et al. (1985) have reported alterations in phototaxis by larval stages of crustaceans as a result of embryonic exposure to a toxicant. Both the level and sign of phototaxis were altered in light-adapted first stage larvae of *P. pugio* after 4-day single pulse exposure of the embryos to DFB. These alterations in phototaxis were shown to be dependent on the DFB concentration and the embryonic stage at exposure

(Wilson et al. 1985). The present study was conducted to determine if and when larval grass shrimp from DFB-treated embryos which exhibit altered phototaxis regain normal pattern of phototaxis during larval development.

## MATERIALS AND METHODS

Ovigerous female grass shrimp *P. pugio* that were induced to spawn in the laboratory (Duke University Marine Laboratory, Beaufort, NC) were sorted according to stage of embryonic development as described by Wilson (1985). Laboratory animals were used in this study because they were relatively homogeneous and gave less variable results than field animals. Only ovigerous females carrying Stage IV embryos (6-day-old; body segmentation stage, at  $25 \pm 1^\circ\text{C}$ ) were used in this study. Earlier studies by Wilson (1985) and Wilson et al. (1985) have shown that Stage IV embryos are the most sensitive embryonic stage and represent a midpoint in the embryonic development of *P. pugio*. The shrimp were placed in large culture dishes (inside diameter = 20 cm) containing 0.5  $\mu\text{g/L}$  of wettable powder (WP-25%) formation of DFB dissolved in 20‰ filtered (to 45  $\mu\text{m}$ ) seawater. Untreated 20‰ filtered seawater served as the control. This test concentration was used because Wilson et al. (1985) have shown that for phototaxis, 0.5  $\mu\text{g/L}$  is the lowest observed effect concentration (LOEC) when various embryonic exposure concentrations were used. The shrimp were maintained at a density of 5 per liter of test solution for 4 days without renewal (single dose exposure). After the 4-day exposure, the shrimp were transferred into clean seawater (20‰), which was changed every day until the eggs hatched. The larvae were then used in phototaxis experiments. The rationale for exposing embryos rather than larvae is that this test protocol, delayed sublethal bioassay (DSB), has been shown to be more sensitive than shrimp or crab larval bioassays (see Wilson 1985 for details). Ovigerous females and larvae were reared in an environmental chamber set at  $25^\circ\text{C}$  and 12L:12D photoperiod, centered at 1200 h. Animals were fed freshly hatched *Artemia* sp. nauplii daily.

Experiments were performed to determine ontogeny of phototaxis of larvae hatched from unexposed embryos (control) and embryos exposed to 0.5  $\mu\text{g/L}$  DFB. The general protocol for all phototaxis experiments was that described by Wilson et al. (1985) with few modifications. Phototaxis was determined by measuring the direction of swimming immediately following light stimulation. Ten to 15 larvae were placed in an acrylic trough measuring 14.9 x 8.3 x 3.5 cm containing approximately 110 ml filtered seawater (20‰). The trough was divided into 5 equal compartments by acrylic partitions which could be raised

or lowered simultaneously. The stimulus light was presented horizontally from a slide projector fitted with a 300 watt incandescent bulb. The light was interference-filtered to 500 nm (7 nm halfbandwidth). This wavelength was selected because it has been shown to be the spectral sensitivity maximum for *P. pugio* (personal communication, John K. Douglas, University of Arizona, Tucson, AZ 85721, unpublished) and *P. vulgaris* (White 1924). Intensity was regulated by neutral-density filters (Detric Optics, Inc.) and measured with a radiometer (from EG&G model 550).

Phototaxis measurements were performed in a photographic darkroom between midnight and 0300 h. This time was chosen to coincide with the time of maximum larval release by laboratory-maintained ovigerous females (personal observations), thereby ensuring that larvae were  $24 \pm 2$  h old when first tested. By monitoring phototaxis at the same time of day for all experiments, complications due to biological rhythms in behavior (see Forward and Cronin 1980) were avoided. Shrimp larvae were light adapted for 4–6 h to 12.53  $\text{Wm}^{-2}$  light intensity (cool-white fluorescent lamps) prior to testing. Ten to 15 larvae were placed in the central compartment of the acrylic trough and allowed to adapt in darkness for 30 s. After this, the partitions were raised gently and the stimulus light turned on simultaneously. Larvae were then stimulated for 60 s then the partitions were lowered and the stimulus light turned off. The number of larvae in each compartment was recorded. Larvae were returned to rearing conditions and tested on subsequent days. A new group of larvae were then introduced into the trough and tested as previously outlined. This procedure was repeated at least 3 times before the neutral density filters were changed to test a different intensity of the stimulus light. Six to 7 different light intensities were tested plus a "dark control" in which the movements of larvae in the test trough were monitored without any stimulus light. Different larvae were used for each stimulus light level. The larvae were fed throughout the phototaxis experiments to reduce the possibility of altered phototaxis due to starvation (Cronin and Forward 1980, Lang et al. 1980). The intensity versus response curves for these larvae were again determined on the second day (i.e., for 2-day-old larvae). Using the same batch of larvae, this procedure was repeated every day up to Day 4 and again on Day 8. Examination of both untreated and treated larvae on Day 4 indicated that they had stalked eyes and thus had molted to the 2nd zoeal stage.

Positive phototaxis was defined as movement towards the light source and negative phototaxis as movement away from the light source. The animals in the 2



compartments closest to the light source were regarded as showing positive phototaxis; those in the 2 compartments farthest from the light source as negatively phototactic. The mean percentage positive and negative response and their standard errors (S.E.) were calculated at each light intensity. For statistical analysis, the percentages were first arcsine transformed. Statistical tests determined the difference between dark control (no light stimulus) response levels due to movement in the test trough in darkness and responses upon stimulation with light. Chi-square tests and analysis of variance were performed on the results as described by Sokal and Rohlf (1981). The level of significance was set at  $P = 0.05$  for all tests.

## RESULTS

### Larvae from Unexposed Embryos

The intensity versus response curves for light-adapted larvae from unexposed embryos during ontogeny are shown (Figure 1). The pattern of phototaxis exhibited by Day 1 larvae (Stage I) remains virtually the same through Day 8 of development. As compared to the dark control level of responsiveness, larvae were positively phototactic ( $P < 0.05$ ; ANOVA) at the stimulation intensity of  $3 \times 10^{-1}$  (days 2, 4, and 8) or at  $3 \times 10^{-2} \text{ Wm}^{-2}$  and higher intensities (Days 1 and 3). Larvae were negatively phototactic ( $P < 0.05$ ; ANOVA) at lower light intensities with the threshold being  $3 \times 10^{-5} \text{ Wm}^{-1}$  for Days 1 to 4 and one log unit higher for Day 8.

There is some indication of increased activity by the larvae with age as evidenced by the increase in the dark control responses of larvae. The positive control (no light present) increased from 26% on Day 1 to 40% on day 8 (Figure 1).

### Larvae from Embryos Exposed to DFB

The ontogenetic changes observed in the photoresponses of light-adapted larvae that hatched from embryos (Stage IV) exposed to  $0.5 \mu\text{g/L}$  DFB are presented in Figure 2. Positive phototaxis was absent (relative to the dark controls) at the stimulation intensities that normally evoked significant positive responses in untreated larvae ( $3 \times 10^{-2} \text{ Wm}^{-2}$  and higher; Figure 1). Compared with Day 1 untreated larvae (Figure 1), the larvae from DFB-treated embryos exhibited negative phototaxis ( $P < 0.05$ ; ANOVA) (Figure 2) over a much wider range of stimulus intensities ( $3 \times 10^{-2}$  to  $10^{-1} \text{ Wm}^{-2}$ ).

By Day 2, the first sign of a return to the normal pattern of phototaxis was evident as seen by an increase in positive phototaxis from the control level on Day 1 to 72% on the second day at  $3 \times 10^{-1} \text{ Wm}^{-2}$  stimulation intensity (Figure 2). The positive responses at  $3 \times 10^{-1} \text{ Wm}^{-2}$  on Days

2 and 3 by treated larvae are not significantly different ( $P > 0.05$ ; chi-square) from each other (Figure 2). At an intensity of  $3 \times 10^{-2} \text{ Wm}^{-2}$ , Days 2 and 3 larvae remained strongly negatively phototactic. However, by Day 4, the larvae exhibited positive phototaxis at both  $3 \times 10^{-2}$  and  $3 \times 10^{-1} \text{ Wm}^{-2}$  (see Figure 2). Thus, the return to normal photoresponse is complete by Day 4 for larvae from embryos exposed to  $0.5 \mu\text{g/L}$  DFB. The response patterns exhibited by 4- and 8-day-old larvae were almost identical. The lowest light intensity evoking positive phototaxis and the highest intensity that evokes negative phototaxis for unexposed and exposed larvae are compared in Table 1. Although these threshold intensities were very different for 1-day-old treated and untreated larvae, they became identical by Day 4.

## DISCUSSION

The phototactic pattern of Stage I larvae from the grass shrimp *P. pugio* has been extensively documented by Wilson (1985) and Wilson et al. (1985). The pattern of phototaxis of light adapted Stage I larvae from untreated embryos was positive phototaxis at high light intensities ( $3 \times 10^{-2}$  and  $3 \times 10^{-1} \text{ Wm}^{-2}$ ) and negative phototaxis at lower light intensities ( $3 \times 10^{-5}$  to  $3 \times 10^{-2} \text{ Wm}^{-2}$ ; Figure 1; Wilson et al. 1985). This pattern of phototaxis persists for larvae from untreated embryos irrespective of the age of the embryos when incubation started in the laboratory (Wilson 1985, Wilson et al. 1985). For larvae that hatched from DFB-treated embryos, both the magnitude and the sign of the photoresponse were altered. Such larvae consistently exhibited negative phototaxis at higher light intensities that normally evoke positive phototaxis ( $3 \times 10^{-2}$  and  $3 \times 10^{-1} \text{ Wm}^{-2}$ ). These alterations in phototaxis varied upon exposing embryos to concentration of DFB ranging from  $0.3$  to  $1.0 \mu\text{g/L}$  (Wilson et al. 1985). However, at exposure concentrations of  $\geq 2.5 \mu\text{g/L}$ , larvae exhibited severe structural abnormalities, and the magnitude of both positive and negative phototaxis was drastically reduced (Wilson 1985).

Results of the present study indicate that for light-adapted Stage I larvae from unexposed embryos, phototaxis remains virtually unchanged during larval development. Both the pattern of the stimulus light intensity versus phototactic response curves and the magnitude of the phototactic responses were similar for all the larval stages tested (up to 8 days old). It should be pointed out that this pattern of phototaxis by light-adapted larvae was also observed up to Day 15 (Wilson unpublished data). However, at the postlarval stage (unpublished data) both positive and negative phototaxis are lost since the animals

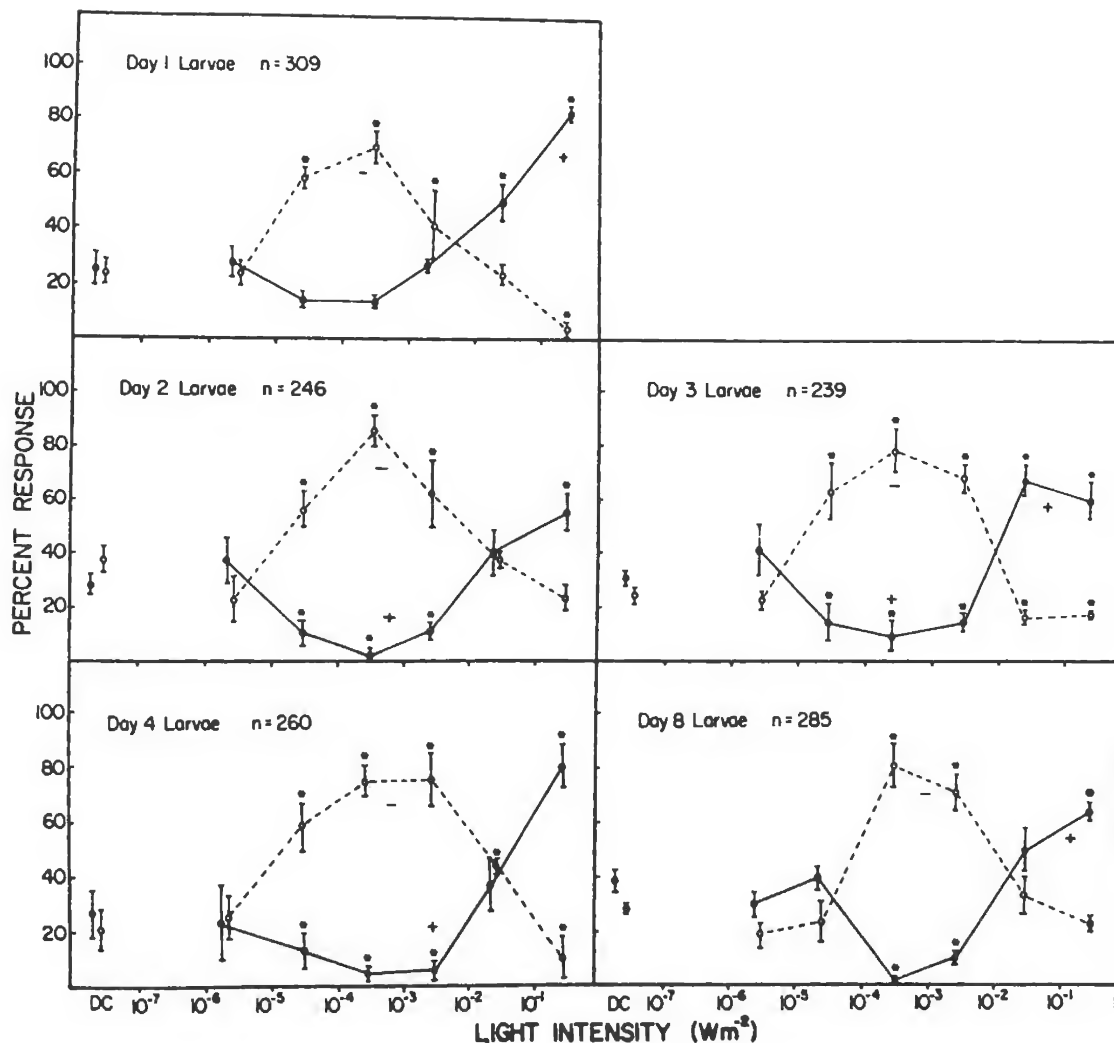
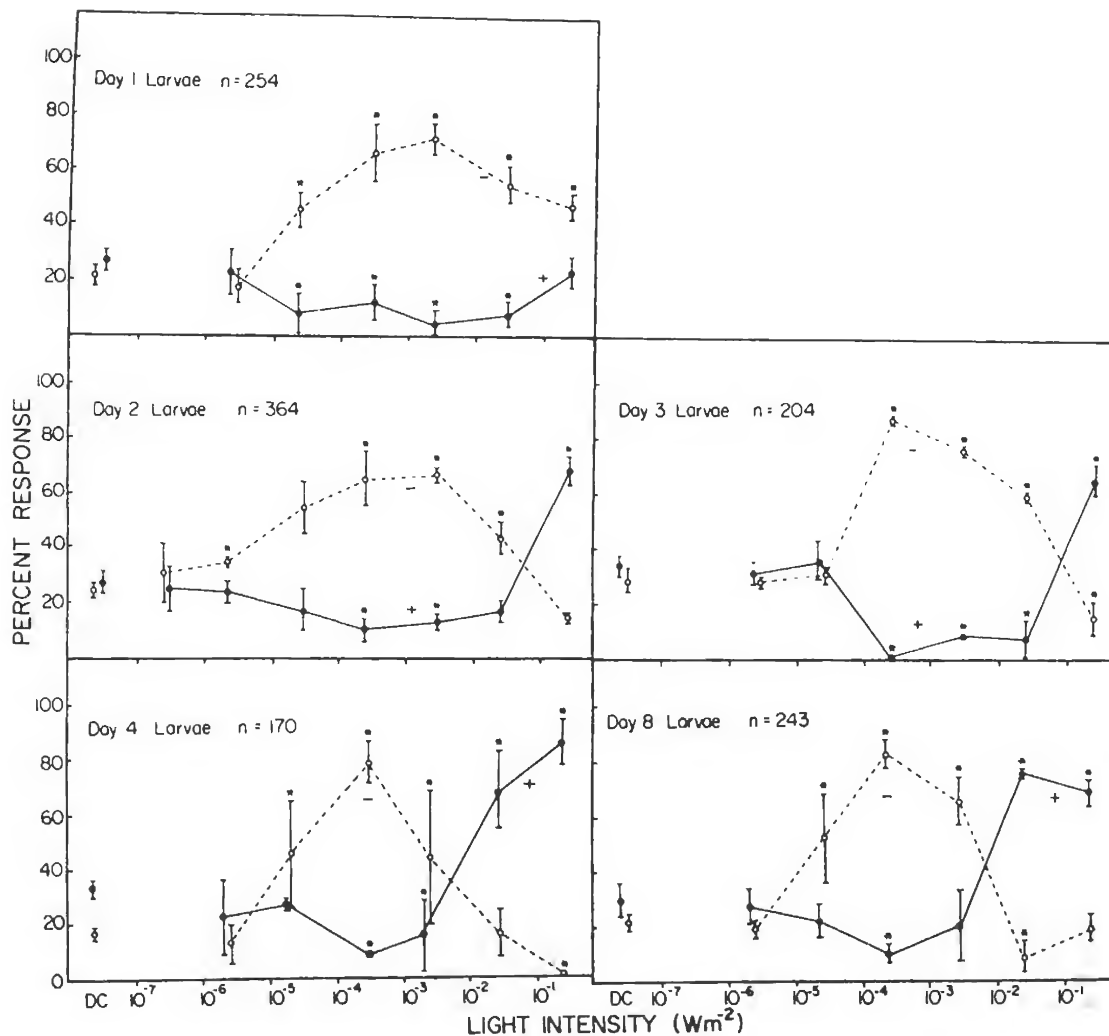


Figure 1. *Palaemonetes pugio*. Intensity versus response curves for different ages of light-adapted larvae hatched from untreated embryos (i.e., incubated in seawater throughout embryonic development). Open circles, dashed lines represent negative phototaxis. Closed circles, solid lines represent positive phototaxis. DC = dark control values for larvae moving to the positive and negative chambers of the test trough in the absence of light. Data points are means  $\pm$  S.E. The sample size (n) for each stimulus intensity was 3. Asterisks indicate means that are significantly ( $P < 0.05$ ) greater or less than the appropriate dark control. Embryos were 6 days old when incubation started.

# ONTOGENY OF PHOTOTAXIS BY GRASS SHRIMP LARVAE



**Figure 2.** *Palaemonetes pugio*. Intensity versus response curves for different ages of light-adapted larvae hatched from embryos that were exposed to 0.5  $\mu g/L$  diflubenzuron starting when they were 6 days old. Open circles, dashed lines represent negative phototaxis. Closed circles, solid lines represent positive phototaxis. DC = dark control values for larvae moving to the positive and negative chambers of the test trough in the absence of light. Data points are means  $\pm$  S.E. The sample size (n) for each light intensity was 3. Asterisks indicate means that are significantly ( $P < 0.05$ ) greater or less than the appropriate dark control.

TABLE 1

Comparison of lowest light intensity that evokes positive phototaxis and highest light intensity evoking negative phototaxis in grass shrimp larvae from untreated control and diflubenzuron (DFB)-exposed embryos. NR is no phototactic response.

Larval Age (Days)	Positive Response (Lowest Intensity) $\text{Wm}^{-2}$		Negative Response (Highest Intensity) $\text{Wm}^{-2}$	
	untreated	DFB-exposed	untreated	DFB-exposed
1	$3 \times 10^{-2}$	NR	$3 \times 10^{-3}$	$3 \times 10^{-1}$
2	$3 \times 10^{-2}$	$3 \times 10^{-1}$	$3 \times 10^{-3}$	$3 \times 10^{-2}$
3	$3 \times 10^{-2}$	$3 \times 10^{-1}$	$3 \times 10^{-3}$	$3 \times 10^{-2}$
4	$3 \times 10^{-2}$	$3 \times 10^{-2}$	$3 \times 10^{-3}$	$3 \times 10^{-3}$
8	$3 \times 10^{-2}$	$3 \times 10^{-2}$	$3 \times 10^{-3}$	$3 \times 10^{-1}$

were unresponsive to even the highest stimulation intensity used ( $3 \times 10^{-1} \text{ Wm}^{-2}$  at 500 nm light). Forward and Costlow (1974) have reported a similar pattern in phototaxis during ontogeny for the mud crab, *R. harrisi*. Both the action spectra and the intensity versus response curves for light- and dark-adapted animals were similar for all zoeal stages. On metamorphosis into the megalopa stage, there was a dramatic change in behavior similar to that reported here for the postlarvae of the grass shrimp. These findings are different from those reported by Welsh (1932) for the mussel crab and by Hunte and Myers (1984) for estuarine amphipods, where changes from positive to negative phototaxis were observed during larval development. In some instances, (e.g. in *Balanus*) there is a change from positive phototaxis in newly hatched nauplii to negative in Stage II and back to positive in the cyprid stage (Thorson 1964).

The lack of ontogenetic changes in phototaxis of *P. pugio* larvae from untreated embryos made it relatively easy to determine when larvae from DFB-treated embryos regained normal photobehavior. By comparing the pattern of the intensity versus response curves for each age of the larvae from untreated and DFB-treated embryos, it was observed that a return to normal photobehavior started with Day 2 larvae and by the time they were 4 days old, the response patterns were similar to that of the untreated group. Thus, it is possible for larvae with altered photobehavior resulting from embryotoxicity of DFB to regain their normal photoresponsiveness within 2 to 4 days if reared in clean seawater during larval development.

Microscopic examination indicated that 4-day-old treated and untreated larvae had molted to the 2nd zoeal stage in the present experiment. Therefore, the change back to normal pattern of phototaxis by light-adapted larvae from DFB-exposed embryos was completed after the larvae molted to the 2nd stage. Although there are reports of altered

phototaxis by crustacean larvae and adults resulting from exposure to toxicant (Bigford 1977, Forward and Costlow 1976, Lang et al. 1980, Moyer and Barthalmus 1979, Wilson et al. 1985), the present study is the first report of re-establishment of normal phototaxis upon removal of the toxicant during larval development.

In untreated Stage I larvae the eyes are sessile with cuticular lens and apposition optics, i.e., the lenses form small inverted images on the rhabdoms (Land 1984, Fincham 1984). For details on the structure and function of grass shrimp eyes, see Parker (1897), Douglass (1986), and Douglass and Forward (1989). Ontogenetic study of the compound eyes of *P. pugio* from larval to postlarval stage shows that the basic morphological and anatomical organization of the eyes remain unchanged throughout larval development (Douglass and Forward 1989). It is therefore not surprising that the photoresponse of untreated larvae remain the same during larval development in this study. The altered photoresponse seen in larvae from DFB-exposed embryos is conceivably the result of structural modification of the visual system of the larvae. Grass shrimp larvae hatched from embryos exposed to  $0.5 \mu\text{g/L}$  DFB have been shown to exhibit slight morphological abnormalities (terata), which also affect swimming speed and vertical distribution in a seawater column (Wilson et al. 1985, Wilson et al. 1987).

Ultrastructural study of the exoskeleton of the mud crab *R. harrisi* by Christiansen and Costlow (1982) revealed that larvae exposed to DFB had disorganized and swollen exocuticle. Since the thickness of the cuticle is the same in *Rhithropanopeus* and *Palaemonetes* (Freeman 1993) and the effects of DFB on larval crustaceans is similar, it can be presumed that larvae from DFB-treated embryos may have swollen and malformed cuticular facets in the eyes. Such swollen cuticular facets may alter the entire optics of the larval eyes and could account for the

observed reversal in phototaxis. In apposition eyes, the cuticular facet acts as a lens which focuses light on the rhabdom (Cronin 1986). Conceivably, when the lens is not properly formed, e.g., has granular disorganized endocuticle (see Mulder and Gijswijt 1973), or is swollen, the amount of light passing through will be reduced. This may explain why exposed larvae responded negatively at light intensities to which they normally reacted positively. Normal phototaxis is restored upon molting probably as a result of formation of new cuticular facets with normal thickness and endocuticle. It is also possible that the distribution of the visual pigments in DFB-treated larvae is altered as a result of biochemical changes. Irrespective of what mechanism caused alteration in phototaxis, it is clear from the present study that normal phototaxis was restored after the larvae molt to the 2nd zoeal stage.

Since larvae were tested in an unnatural light field (e.g. Forward 1985), relating phototaxis to actual behavior in nature is difficult. Nevertheless, the results do indicate photobehavior was altered by exposure to DFB, and thus, aspects of larval ecology that depend on photobehavior would be altered. Photobehavior is involved in diel vertical migration of the larvae, and hence their temporal vertical distribution in an estuary (Allen and Barker 1985) could be altered. Since their vertical distribution affects horizontal transport, recruitment to the adult population would be affected. The ability to avoid predators could also be reduced by alterations in photobehavior, since the negative phototaxis participates in a predator avoidance shadow response (Forward 1977). Also, Douglass et al. (1992) demonstrated that *P. pugio* larvae have endogenous phototaxis rhythm, which if altered would change the photoresponse pattern throughout the tidal cycle in an estuary. Thus, the survival potential of the shrimp population could be reduced by alteration in larval photobehavior.

In summary, the pattern of phototaxis by grass shrimp larvae from untreated embryos remains unchanged during larval development. This pattern consists of a positive phototaxis at high light intensity ( $\geq 3 \times 10^{-2} \text{ Wm}^{-2}$ ) and negative phototaxis at lower intensities ( $\leq 3 \times 10^{-3} \text{ Wm}^{-2}$ ). Although larvae from DFB-treated embryos had altered phototaxis, photobehavior was gradually restored as the larvae developed in clean water, and restoration was complete upon molting to the 2nd zoeal stage. Hence, altered phototaxis as a result of embryotoxicity to DFB is only temporary in grass shrimp larvae.

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Parasitization of *Callinectes rathbunae* and *Callinectes sapidus* by the Rhizocephalan Barnacle *Loxothylacus texanus* in Alvarado Lagoon, Veracruz, Mexico

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## PARASITIZATION OF *CALLINECTES RATHBUNAE* AND *CALLINECTES SAPIDUS* BY THE RHIZOCEPHALAN BARNACLE *LOXOTHYLACUS TEXANUS* IN ALVARADO LAGOON, VERACRUZ, MEXICO

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**ABSTRACT** *Callinectes rathbunae* and *Callinectes sapidus* in Alvarado Lagoon, Mexico, were sampled monthly for one year to determine the extent of parasitization by the rhizocephalan cirripede *Loxothylacus texanus*. Prevalence levels, host sex ratio, carapace width-weight variation, and distribution of the number of parasites among hosts were analyzed. *Loxothylacus texanus* was present almost exclusively in *C. rathbunae* with a mean prevalence of 7.58%, while less than 1% of all *C. sapidus* were parasitized. *Callinectes rathbunae* constitutes a new host record for this parasite. A study of infection revealed significant variation in prevalence and host size throughout the study period. The sex ratio of parasitized crabs differed from that of the total sample with males being parasitized more often, and the comparison of carapace width-weight relationships revealed lower weights of parasitized crabs.

### INTRODUCTION

A number of studies on the rhizocephalan barnacle *Loxothylacus texanus* Boschma parasitizing the blue crab, *Callinectes sapidus*, in the Gulf of Mexico have been published in the last several decades describing: temporal and geographic variation in prevalence (Adkins 1972, Hochberg et al. 1992, Lázaro-Chávez et al. 1996), host size distribution (Christmas 1969, Adkins 1972, Ragan and Matherne 1974), morphological modifications of hosts (Reinhard 1950, Alvarez and Calderón 1996), and the relationship between host size and parasite size (Wardle and Tirpak 1991). The interest in the effect of this parasite on the commercially important blue crab is renewed whenever a new outbreak is detected (Wardle and Tirpak 1991) and few long-term prevalence records have been kept (O'Brien and Overstreet 1991).

Until recently, no published information existed on the extent of the blue crab-rhizocephalan interaction in Mexican waters of the Gulf of Mexico, although parasitized crabs have long been recognized by local fishermen. *Loxothylacus texanus* is well established in the Gulf of Mexico occurring in *C. sapidus* from southern Florida to Campeche (Hochberg et al. 1992, Alvarez and Calderón 1996) and in *C. rathbunae* from central Veracruz to Términos Lagoon, Campeche (Alvarez and Calderón 1996). *Loxothylacus texanus* has been reported outside the Gulf of Mexico in *Callinectes larvatus* in the Canal Zone, Panama (Boschma 1950), and in *C. sapidus* at 4 sites along the Caribbean coast of Colombia (Young and Campos 1988, Alvarez and Blain 1993).

A one year survey for *L. texanus* by monthly samplings of *C. rathbunae* and *C. sapidus* was conducted in Alvarado

Lagoon, southern Veracruz (Figure 1), to determine parasite prevalence levels, host species selectivity, host carapace width-weight variation, and distribution of number of parasites per host.

### MATERIALS AND METHODS

Monthly samples (12) of *Callinectes* spp. from Alvarado Lagoon were examined from November 1995 to November 1996 (except October). Data were obtained from the catch of local fishermen. Their catch was collected and processed in the "Cooperativa Primero de Abril", in Alvarado, Veracruz. Crabs were identified, measured (carapace width), weighed, and sexed. Male crabs were classified as parasitized by *L. texanus* if they presented an abnormally shaped abdomen and atrophied first pleopods. Female crabs were considered parasitized if they presented atrophied pleopods with mature abdominal shape. Crabs of both genders were considered parasitized if they exhibited the parasite externa, or bore scars in the abdomen where externa had been attached. All crabs in which morphological modifications were detected, but which did not bear an externa were labeled as "feminized". When present, externa were counted and classified as immature (small, mantle opening not developed) or mature (full-sized, mantle opening fully developed). An average of 177 crabs was examined monthly.

Statistical analysis of data included: Student's t-test, analysis of variance (ANOVA), analysis of covariance (ANCOVA), G-test of independence, and Chi-square test. All crab sizes are reported in millimeters (mm) and weights in grams (g); mean values are followed by  $\pm$  one standard error.



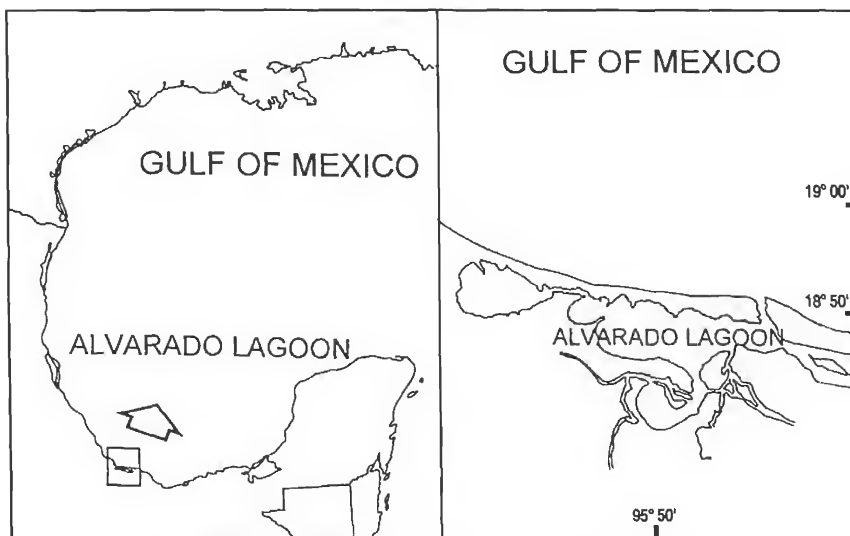


Figure 1. Location of Alvarado Lagoon, southern Veracruz.

## RESULTS

A total of 2,132 crabs was examined, which included 668 *C. sapidus* and 1,464 *C. rathbunae*. Overall prevalences were 0.75% (5 crabs parasitized) in *C. sapidus* and 7.58% (111 crabs parasitized) in *C. rathbunae*. The 5 parasitized *C. sapidus* were collected in January (1), March (3), and November (1). Prevalence in *C. rathbunae* varied between 2% and 12% in ten of 12 collections; maximum prevalence was recorded in December (23.68%) whereas no parasitized crabs were collected in March (Figure 2).

One male and 4 female *C. sapidus* were found to be parasitized. Statistical analysis was not performed on this species due to small sample size. Parasitized *C. rathbunae* included 62 males and 49 females (1.26 males per female), while the unparasitized population was represented by 549 males and 804 females (1.46 females per male). Comparison of these values shows that the parasitized condition was not independent of sex (G-test,  $P < 0.005$ ), and that males were parasitized more often than females.

Mean size of parasitized crabs varied significantly between host species (t-test). In *C. sapidus* the overall

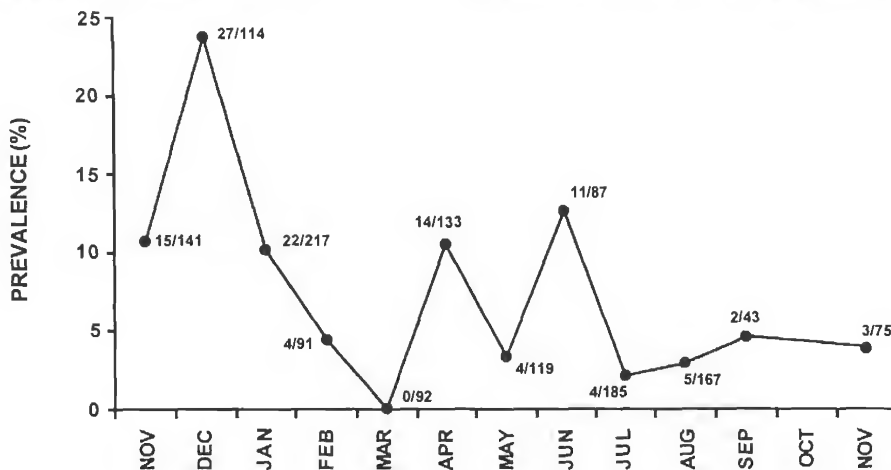


Figure 2. Prevalence of *Loxothylacus texanus* in *Callinectes rathbunae* from Alvarado Lagoon (1995-1996). Sample size indicated as number of parasitized crabs/total examined.

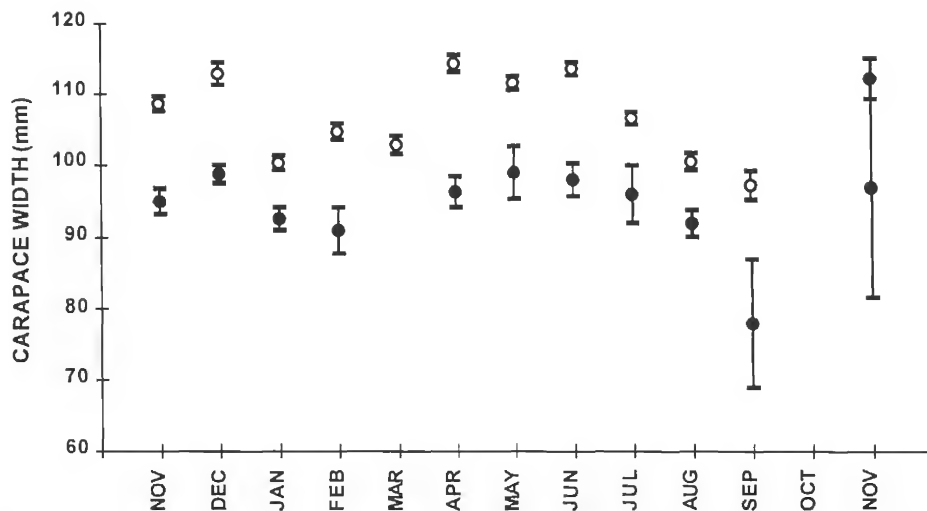


Figure 3. Mean size (CW) of parasitized (solid circles) and unparasitized (open circles) *Callinectes rathbunae* in Alvarado Lagoon (1995-1996); error bars represent  $\pm$  one standard error.

mean was  $111.60 \pm 6.01$  mm ( $n = 5$ , range 92-130 mm), while in *C. rathbunae* it was  $95.48 \pm 0.80$  mm ( $n = 111$ , range 69-122 mm). Due to the small number of parasitized *C. sapidus*, no further analyses were performed. Mean size for parasitized *C. rathbunae* was less than that of the unparasitized population ( $99 \pm 3.61$  mm in May to  $78 \pm 9.04$  mm in September); however, no significant differences were encountered (ANOVA with months as treatments) (Figure 3). Mean size of parasitized male ( $94.25 \pm 0.89$  mm,  $n = 60$ , range 78-110 mm) and female crabs ( $97.02 \pm 1.4$  mm,  $n = 49$ , range 69-122 mm) did not differ statistically (t-test).

Carapace width-weight relationships for *C. rathbunae* were significant for both parasitized (%  $y = 1.62 X - 100.46$ ,  $n = 54$ ,  $r = 0.68$ ,  $P < 0.001$ ; &  $y = 0.84 X - 25.95$ ,  $n = 41$ ,  $r = 0.46$ ,  $P < 0.01$ ; Figure 4) and unparasitized crabs (%  $y = 2.12 X - 143.55$ ,  $n = 116$ ,  $r = 0.93$ ,  $P < 0.001$ ; &  $y = 1.87 X - 125.23$ ,  $n = 142$ ,  $r = 0.93$ ,  $P < 0.0001$ ; Figure 5). The slopes of 4 regressions (ANCOVA with carapace width as covariate,  $F_{(1,185)} = 26.09$ ,  $P < 0.0001$ ) were not homogeneous even when the weight values of the 4 categories of crabs overlapped extensively in the 80-110 mm of carapace width interval. Unparasitized males had the highest slope, followed respectively by unparasitized females, parasitized males, and parasitized females.

Of the 111 parasitized *C. rathbunae*, 19 (17.12%) were feminized (12 males and 7 females), and 92 (82.88%) bore externa (50 males and 42 females). The number of parasite externa per host varied from one to four: 64.86% had one, 14.41% had two, 2.7% had three, and 0.9% had four. The

observed pattern did not conform to a Poisson (random) distribution (Table 1) and may reflect an aggregated pattern since the observed frequencies of multiple externa are much higher than expected and the coefficient of dispersion is greater than one ( $CD = 1.45$ ). Throughout the year, the relative frequencies of internal (feminized hosts), immature, and mature parasites did not seem to follow a defined pattern (Figure 6).

## DISCUSSION

In Alvarado Lagoon, *C. rathbunae* was the main host for *L. texanus*, even though *C. sapidus* was locally abundant. *Callinectes rathbunae* was parasitized by *L. texanus* only south of Casitas, Veracruz (Alvarez and Calderón 1996). To the north, throughout roughly half of its distribution range, the *C. rathbunae* population was not found to carry *L. texanus*. Examination of collections of crabs from Tamiahua Lagoon, north of Casitas, has shown that while *L. texanus* prevalence in *C. sapidus* can reach 51.5%, no *C. rathbunae* are known to be parasitized in the area (Lázaro-Chávez et al. 1996). In contrast, in Alvarado Lagoon, only 5 *C. sapidus* were found parasitized throughout the present study, while prevalence in *C. rathbunae* reached 23.68%.

Most rhizocephalans exhibit a loose specificity, commonly parasitizing 2 or more closely-related host species, often of the same genus (Høeg 1995). Conditions that may promote new host species acquisition when a host species and a closely related potential host species

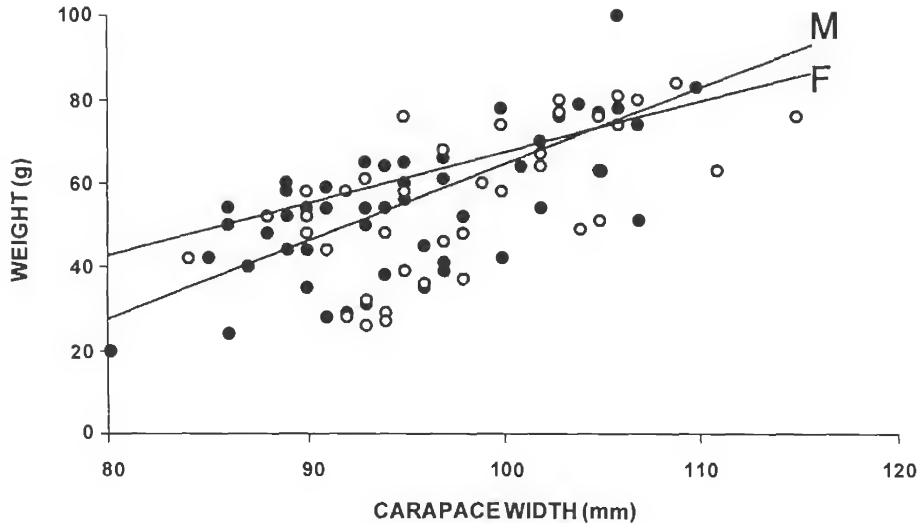


Figure 4. Carapace width-weight relationship of parasitized *Callinectes rathbunae* in Alvarado Lagoon (white circles = females, black circle = males).

occur sympatrically have not been explored. In *Loxothylacus panopaei*, which parasitizes 4 species of xanthid crabs along the east coast of North America, the differential levels of parasitization in each host species may be due to subtle differences in the spatial distribution within the estuary as well as to that of infective parasite larvae (Walker et al. 1992, Alvarez 1993). Within the Gulf of Mexico, the apparent abandonment by *L. texanus* of *C.*

*sapidus* and its subsequent acquisition of *C. rathbunae* cannot be explained with the available data. However, the observed pattern could also be the result of *L. texanus* parasitizing the less desirable *C. sapidus* where *C. rathbunae* is not available.

*Loxothylacus texanus* occurs outside the Gulf of Mexico southward to Colombia (Young and Campos 1988, Alvarez and Blain 1993). In Panama, *C. larvatus* has been

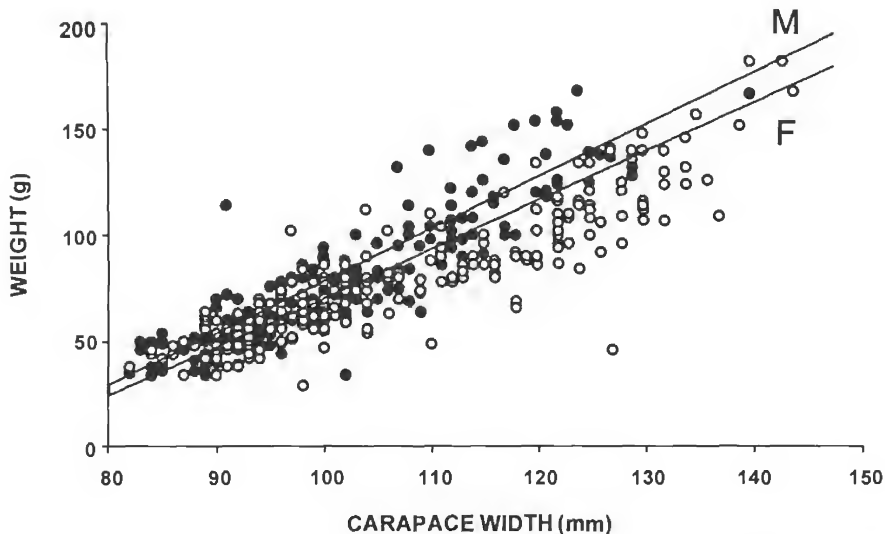


Figure 5. Carapace width-weight relationship of unparasitized *Callinectes rathbunae* in Alvarado Lagoon (white circles = females, black circles = males).

TABLE 1

Distribution of externae of *Loxothylacus texanus* in 1,445 *Callinectes rathbunae* from Alvarado Lagoon. Feminized crabs ( $n = 19$ ) with no externae are not included. Observed frequencies are compared (Chi-square test) to the expected frequencies of a Poisson (random) distribution.

Number of externae per host	Observed frequencies	Expected frequencies	(O - E) <sup>2</sup> /E
0	1,353	1,332.61	0.312
1	72	107.94	11.966
2	16	4.37	30.951
3	3	0.118	70.38
4	1	0.0024	414.669
Total	1,445	1,445.04	$\chi^2 = 528.288$ , $p < 0.0001$

reported as a host species for *L. texanus* (Boschma 1950); unfortunately no other data from the region are available, and the parasitization of other species of *Callinectes* by *L. texanus* cannot be ruled out.

As has been reported in other studies on blue crabs parasitized by *L. texanus* in the Gulf of Mexico, in Alvarado Lagoon there is significant variation in prevalence throughout the annual cycle. This is probably due to the varying intensity of host recruitment synchronized with high temperatures and the parasite's reproductive activity

(Hochberg et al. 1992, Lázaro-Chávez et al. 1996). Maximum prevalences of *L. texanus* in Alvarado Lagoon (3.09% in *C. sapidus* and 23.68% in *C. rathbunae*) are low and intermediate, respectively, compared to those from other reports from the Gulf of Mexico (Table 2). Mean prevalence of *L. texanus* in *C. sapidus* in the present study is extremely low (0.5%), while in *C. rathbunae* it can be considered high (6.28%). The size ranges of parasitized crabs of both host species in Alvarado Lagoon are intermediate between the smaller parasitized crabs from Louisiana and Texas and

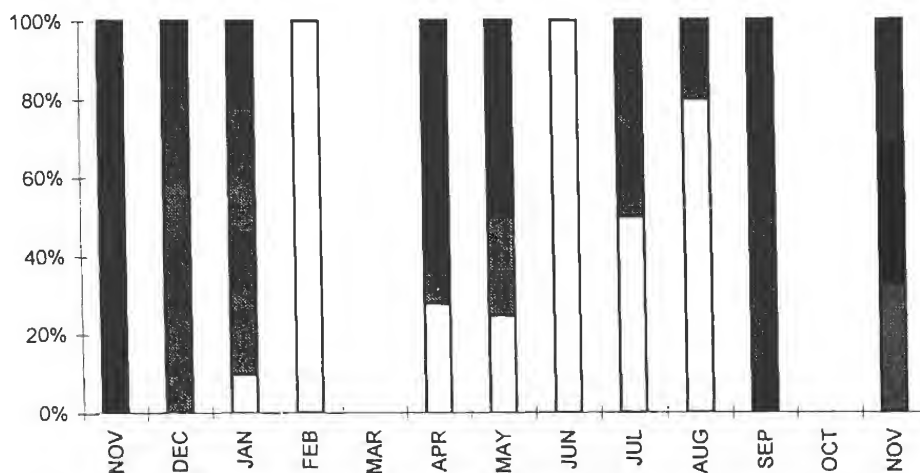


Figure 6. Frequency distribution of *Loxothylacus texanus* in *Callinectes rathbunae* by developmental stage: white bars represent internal parasites (feminized hosts), gray bars represent immature parasites, and black bars represent mature externae. In March 1996, no parasitized crabs were found in the sample. In October 1996, no sample was taken.

TABLE 2

Mean and maximum *Loxothylacus texanus* prevalence and host size range variation of *Callinectes sapidus* and *Callinectes rathbunae* in the Gulf of Mexico; only externae bearing crabs are considered.

Authority	Locality	Host Species	Mean prevalence (%) $\pm$ 1 s.d.	Maximum prevalence (%)	Host size range (mm)
Adkins, 1972	Louisiana, USA	<i>C. sapidus</i>	4.83 $\pm$ 4.8	17.10	30-95
Wardle and Tirpak, 1991	Galveston, Texas, USA	<i>C. sapidus</i>	8.22 $\pm$ 13.7	53.00	43-100
Hochberg et al., 1992	west coast of Florida, USA	<i>C. sapidus</i>	1.40 $\pm$ 1.3	5.10	35-170
Lázaro-Chávez et al., 1996	Tamiahua Lagoon, Mexico	<i>C. sapidus</i>	17.6 $\pm$ 19.7	51.50	45-115
Present study	Alvarado Lagoon, Mexico	<i>C. sapidus</i>	0.50 $\pm$ 1.06	3.09	95-130
Present study	Alvarado Lagoon, Mexico	<i>C. rathbunae</i>	6.28 $\pm$ 6.51	23.68	69-122

the large parasitized individuals found in Florida (Table 2). No pattern of variation associated with geographic distribution is apparent, except that the smallest parasitized crabs occur in the northern Gulf of Mexico.

Although an abnormal abdominal shape combined with atrophied pleopods in *C. sapidus* and *C. rathbunae* are unmistakable signs of parasitization by *L. texanus*, reported prevalence values are mostly based on externae-carrying crabs (Reinhard 1950, Alvarez and Calderón 1996). In Alvarado Lagoon 17.12% of all parasitized crabs showed signs of parasitization but did not bear externae, and were classified as feminized, while in Tamiahua Lagoon, almost half (48%) of all parasitized crabs were feminized (Lázaro-Chávez et al. 1996). These 2 studies show that the margin of error of prevalence estimates that do not consider feminized crabs can be considerable.

The sex ratio of parasitized *C. rathbunae* in Alvarado Lagoon suggests that males are preferentially parasitized. No explanation for this biased sex ratio is apparent, since there is no evidence that infective female cyprid larvae show any selective behavior, at least in *L. panopaei* (Alvarez et al. 1995). In contrast, in Tamiahua Lagoon, although males were more abundant, female *C. sapidus* were parasitized more often (Lázaro-Chávez et al. 1996).

The number of *C. rathbunae* with multiple externae of *L. texanus* occurred in a higher proportion than expected under a random distribution. No mechanism other than chance encounters between infective cyprid larvae and susceptible hosts is currently known to determine the number of parasite externae that emerge from a single host (Walker et al. 1992).

#### ACKNOWLEDGMENTS

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## A Survey of the Reef-Related Medusa (Cnidaria) Community in the Western Caribbean Sea

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## A SURVEY OF THE REEF-RELATED MEDUSA (CNIDARIA) COMMUNITY IN THE WESTERN CARIBBEAN SEA

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**ABSTRACT** The species composition, distribution, and abundance of medusae collected during a 4-day plankton survey in a reef system of the Mexican Caribbean were studied. Highest mean medusae abundance was observed over the fore-reef zone and in daytime samples. Lowest abundances occurred in the reef lagoon and at dusk. Seventeen species were identified, with *Liriope tetraphylla*, *Aglaura hemistoma*, *Cubaia aphrodite*, and *Sarsia prolifera* being the most abundant. They belong to a group of medusae dominant along the world's second largest barrier reef. Cluster analysis revealed primary (fore-reef) and secondary (reef lagoon, channel) oceanic groups, showing the strong oceanic influence along and across the reef system. Day-to-day variation in the reef medusan community seemed relatively unimportant. The community structure of the reef medusa fauna appeared to be quite uniform despite the expected migratory behavior of these predators, tidal exchange across the reef, introduction of oceanic species, and time of day. The species composition was most closely related to that of the Campeche Bank and oceanic Caribbean waters. Dominance of oceanic medusae within the reef lagoon was attributed to the narrowness of the continental shelf and the mesoscale hydrological features of the zone.

### INTRODUCTION

The medusa fauna of coastal, neritic and oceanic waters of the Northwestern Tropical Atlantic has been investigated by several surveys (Phillips 1972, Burke 1975, Segura-Puertas 1991, 1992, Segura-Puertas and Ordóñez-López 1994, Suárez-Morales et al. 1997, Suarez-Morales et al. 1998). However, relatively little emphasis has been placed on coastal environments, where medusae can play a relevant role as predators in the zooplankton food webs (Raymont 1983). Studies dealing with these cnidarians have been developed in estuarine and littoral systems of the Mexican Caribbean (Collado et al. 1988, Zamponi et al. 1990, Zamponi and Suárez-Morales 1991, Suárez-Morales et al. 1998). Along this coast runs the world's second largest barrier reef system (Jordán 1993). Coral reef zooplankton has been surveyed mainly for the most abundant groups such as copepods (Renon 1977, 1993, McKinnon 1991), but not for the less numerous zooplankters of a higher trophic level, such as medusae. There are no previous works dealing with the medusa fauna dwelling in this Mexican reef system. The closest regional antecedent for reef-related medusae is the qualitative survey of Larson (1982) from samples collected in the Carrie Bow Cay reef area off Belize.

This study describes changes in the numerical abundance, composition and diversity of the reef-related medusa fauna of the Mahahual reef system, Mexican Caribbean Sea. The survey comprised a 4-day period, (30 December 1990-2 January 1991), and describes the small-scale space and time variation of the medusan community.

Previous works on the plankton of this reef area refer to zooplankton groups (Castellanos and Suárez-Morales 1997) and to ichthyoplankton (Vásquez-Yeomans et al. 1998).

### Study Area

The Mahahual reef area lies between 18°43' and 18°46'N and 87°42' and 87°42'27"W, on the southern portion of the Mexican coast of the Caribbean Sea (Figure 1). The entire coast receives the influence of Caribbean waters before flowing into the Gulf of Mexico through the Yucatan Channel. The shelf is narrow along this coast and depth increases rapidly offshore (Merino and Otero 1991). A large barrier reef runs along the Mexican Caribbean, from Isla Contoy in the north down through the Belizean coast (Jordán 1993). Mahahual is a small fishing village located on the southern portion of the Yucatan eastern coast. In this area the reef barrier forms a shallow (1.5 m) and narrow (30-180 m) reef lagoon. Benthic vegetation within the lagoon is dominated by beds of *Thalassia testudinum*. Coral cover is minimal along the shallow portions of the lagoon, but increases towards the fore-reef. Surface water temperature is highest in July-August (32°C), and lowest in December-January (21°C). Mean annual salinity along this coast varies within the 32-36‰ range. Oceanographic conditions over this zone are influenced by the Yucatan Current, which flows northward and by a coastal counter current which flows southward. Interaction of both currents produces inshoreward, semi-circular trajectories of drifting objects (Merino 1986). This flow, coupled with tidal currents and turbulence, seems to be the most relevant hydrological phenomenon affecting the reef zooplankton (Suárez-Morales and Rivera-Arriaga 1998).



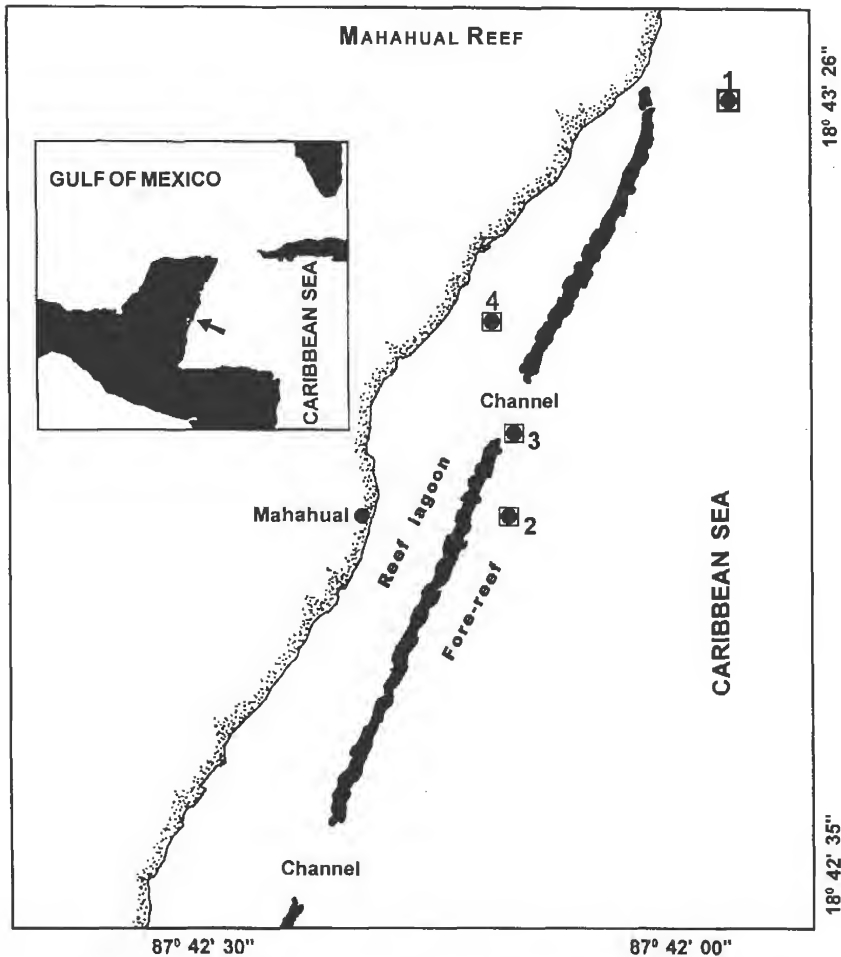


Figure 1. Surveyed area with zooplankton sampling stations, Mahahual reef zone, Mexican coast of the Caribbean Sea.

#### MATERIALS AND METHODS

A 4-day zooplankton sampling program was carried out from 30 December 1990 to 2 January 1991, during the full moon. Stations were located to investigate the three main reef-related zones: fore-reef (FR), Stations 1 and 2; channel (CH), Station 3; and reef lagoon (RL), Station 4 (Figure 1). Daytime sampling was made hourly between 0700 and 1200; evening (dusk) samples were collected between 1730 and 1930. No night collections were made on Day 4. Zooplankton was collected by surface hauls (0–50 m) using a square-mouthed (0.45 m per side) standard plankton net (0.3 mm mesh). This gear allowed collection of small and medium-sized medusae. A digital flowmeter was attached to the net mouth to estimate the volume of water filtered. The mean amount of water filtered during

each trawl was 160 m<sup>3</sup>. At least one replicate tow was performed at each sampling station. Zooplankton samples were fixed and preserved in buffered 4% formaldehyde solution (Smith and Richardson 1979). Medusae were sorted from the entire sample and then identified and counted to obtain the species density (org./100 m<sup>3</sup>). Zooplankton density data were not significantly different among collections (Vásquez-Yeomans et al. 1997). Shannon-Wiener's Diversity Index (bits/individual, which represents the degree of uncertainty about the identity of a given species) and the Index of Importance Value (IIV, a dominance measurement) were estimated for each collection. The Bray-Curtis Similarity Index (Ludwig and Reynolds 1988) was used in the construction of a dendrogram clustering the stations. These calculations were performed with the aid of the ANACOM software computer program (De la Cruz 1994).

## RESULTS

Conditions throughout the surveyed period were quite uniform. Mean surface temperature during the surveyed period ranged from 26° to 28°C. Salinity averaged 36‰, and ranged from 34 to 38‰.

Total medusa densities showed temporal variation through the survey period. Highest total mean densities were recorded during the morning of the first day, the highest two being at Station 2 (578 org./100 m<sup>3</sup>), and at Station 1 (469 org./100 m<sup>3</sup>), both representing the fore-reef zone. Values at the other localities ranged from 7 to 280 org./100 m<sup>3</sup>. Highest mean medusae density occurred in Day 1 over the fore-reef (Station 2, 421 org./100 m<sup>3</sup>).

Overall data for the three reef zones considered herein showed that medusae were most abundant over the fore-reef (mean density 185 org./100 m<sup>3</sup>), followed by the channel (18 org./100 m<sup>3</sup>) and by the reef lagoon (16.7 org./100 m<sup>3</sup>). Up to 87% of the total medusae numbers occurred over the fore-reef, and only 4% in the reef lagoon. Total density was 1.4 times higher in the morning (91 org./100 m<sup>3</sup>) than at dusk (67 org./100 m<sup>3</sup>), with 64% of the individuals being collected during daytime samplings. Over the fore-reef, density values at daytime (190 org./100 m<sup>3</sup>) and at dusk (176 org./100 m<sup>3</sup>) were similar. At the reef lagoon, values were 28 org./100 m<sup>3</sup> (AM) and 6 org./100 m<sup>3</sup> (PM); at the channel zone values were 18.4

and 15.2, respectively (Figure 2). Overall mean density varied day to day. Values recorded were as follows: Day 1, 135 org./100 m<sup>3</sup>; Day 2, 54.35 org./100 m<sup>3</sup>; Day 3, 45.1 org./100 m<sup>3</sup>; Day 4, 97.6 org./100 m<sup>3</sup>. Up to 40% of the total medusan numbers were collected during Day 1, 13% in Day 2, 19% in Day 3, and 28% in Day 4 (only AM).

A total of 17 medusan species were identified (Table 1). The most abundant, *Liriope tetraphylla* (Chamisso and Eysenhardt 1821), accounted for 41% of the medusae, with a mean density of 33.3 org./100 m<sup>3</sup>. Also abundant were *Aglaura hemistoma* Péron and Lesueur 1810 (22%; 17.8 org./100 m<sup>3</sup>), *Cubaia aphrodite* Mayer 1894 (11.6%; 9.4 org./100 m<sup>3</sup>), *Sarsia prolifera* Forbes 1848 (8.2%; 6.6 org./100 m<sup>3</sup>), and *Obelia* sp. (7.11%; 5.7 org./100 m<sup>3</sup>). These five comprised about 90% of the total overall medusan catch. The relative abundance, estimated density, and frequency of all the medusan species recorded in the area are presented in Table 1.

*Liriope tetraphylla* showed an overall mean density in daytime samples of 48 org./100 m<sup>3</sup>, with lower values in dusk samples (40 org./100 m<sup>3</sup>). The same tendency in day vs dusk samples was observed for *Obelia* sp., 12 org./100 m<sup>3</sup> vs 4 org./100 m<sup>3</sup>; *Clytia folleata* (McCrady 1859), 5.7 org./100 m<sup>3</sup> vs 1.5 org./100 m<sup>3</sup>; and *S. prolifera*, 7.8 org./100 m<sup>3</sup> vs 1.8 org./100 m<sup>3</sup>. Values for *A. hemistoma* were equal in day (17.25 org./100 m<sup>3</sup>) and night samples (18.5 org./100 m<sup>3</sup>).

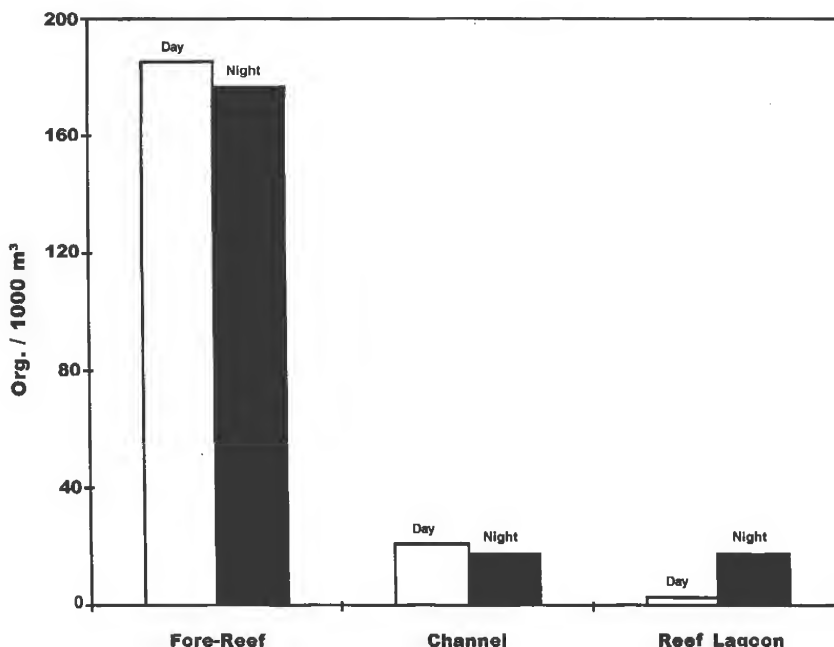


Figure 2. Mean day/night densities (org./100m<sup>3</sup>) of medusae in the three reef-related environments.

*Liriope tetraphylla* was most abundant at the fore-reef. More than 90% of the total numbers of this species occurred in this environment. Only 8.3% occurred in the channel, and the remaining 1.4% reached the lagoon. *Aglaura hemistoma* was collected only at the fore-reef. *Cubaia aphrodite* was most abundant at the fore-reef (57%), and was more abundant at the channel zone (27%) than at the reef lagoon (15%). *Sarsia prolifera* occurred mostly over the fore-reef (80.6%), and was scarce at the channel zone (15%) and the reef lagoon (4.3%).

Several species occurred in either day or dusk samples, and in a specific environment. Occurring only in fore-reef samples at dusk were *Podocoryne minima* (Trinci 1903), *Amphinemadinema* (Péron and Lesueur 1809) and *Halitiara formosa* Fewkes 1882. *Amphinema rugosum* (Mayer 1900) and *Cunina octonaria* (McCradly 1852) were recorded only in fore-reef day time samples. *Halocordyle disticha* (Goldfuss 1820) was observed only in the reef lagoon at dusk.

The species richness was highest at the fore-reef, where 16 out of the 17 medusa species were recorded. Only three species (*L. tetraphylla*, *S. prolifera*, and *C. aphrodite*) were recorded in the channel zone, and only five were observed

in the reef lagoon (*L. tetraphylla*, *C. aphrodite*, *H. disticha*, *Zanclus costatus*, and *S. prolifera*). Overall diversity (Shannon-Wiener) was highest at the fore-reef (1.66 bits/ind.). In this environment, day samples were more diverse (1.84 bits/ind.) than those collected at dusk (1.38 bits/ind.). The reef lagoon (0.4 bits/ind.) and the channel zones (0.6 bits/ind.) showed lower overall diversity values.

Clustering with the Bray-Curtis Index produced a dendrogram (Figure 3) in which two large groups of stations were defined. One group included all the fore-reef stations, and in the other group the remaining stations (reef lagoon and channel) were clustered and mixed.

## DISCUSSION

Only 44% of the species recorded at Mahahual have been previously reported from the reef area off Belize (Larson 1982), while 50% are known from neritic and oceanic waters of the Gulf of Mexico (Phillips 1972, Burke 1975), and 72% from the Campeche Bank and the Mexican Caribbean (Phillips 1972, Zamponi et al. 1990, Zamponi and Suárez-Morales 1991, Segura-Puertas 1992, Segura-Puertas and Ordóñez-López

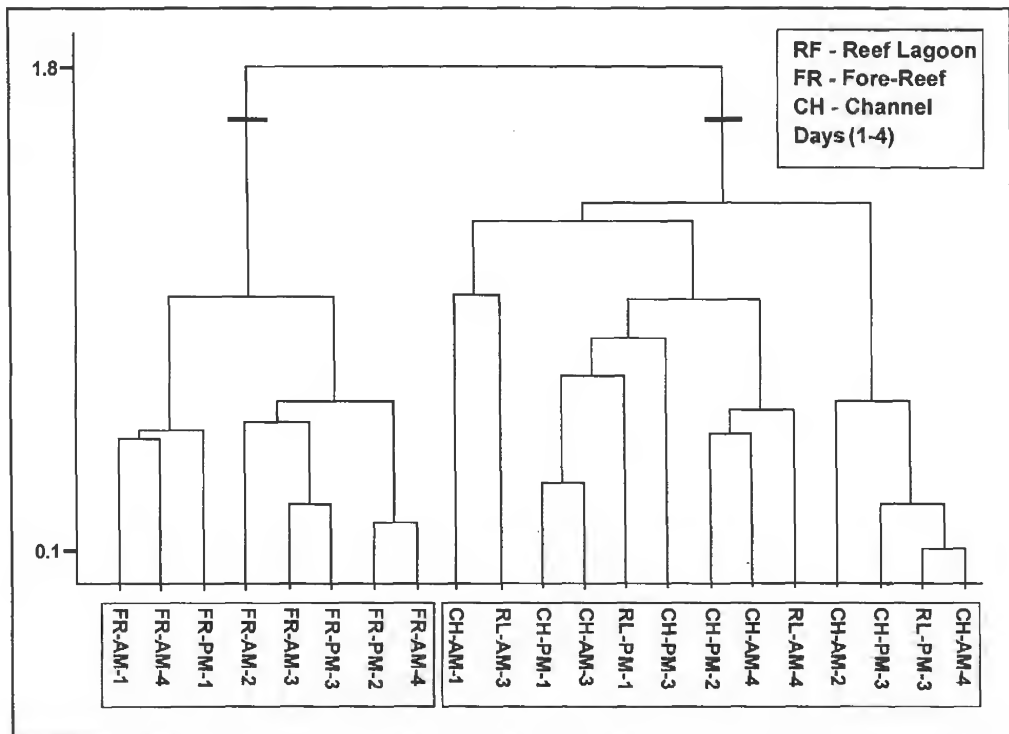


Figure 3. Dendrogram from clustering by Bray-Curtis Index showing distribution of the clusters in the three reef-related environments during the surveyed period.

TABLE 1  
Medusan species density (org./100m<sup>3</sup>) by environment, sampling day, and time of day at Mahahual

Station/Time/Species	30 December 1990						31 December 1990						1 January 1991						2 January 1990			Total
	FR AM	FR PM	CH AM	CH PM	RL PM	RL PM	FR AM	FR PM	CH AM	CH PM	CH PM	FR AM	FR PM	CH AM	CH PM	RL AM	RL PM	CH AM	FR AM	FR PM	RL AM	
<i>Liriope tetraphylla</i>	88	195	0	18	5		15	20	0	5		87	55	35	6	0	0	0	0	0	0	615
<i>Aglaura hemistoma</i>	14	25	0	0	0		28	111	0	0		49	31	0	0	0	0	0	56	0		314
<i>Obelia</i> sp.	90	25	0	0	0		0	0	0	0		2	0	0	0	0	0	0	2	0		119
<i>Clytia folleata</i>	42	8	0	0	0		2	1	0	0		0	0	0	0	0	0	0	3	0		56
<i>Clytia mccrady</i>	0	0	0	0	0		0	0	0	0		6	6	0	0	0	0	0	0	0		12
<i>Carybdea marsupialis</i>	4	3	0	0	0		0	3	0	0		0	0	0	0	0	0	0	0	0		10
<i>Podocoryne minima</i>	0	6	0	0	0		0	0	0	0		0	0	0	0	0	0	0	0	0		6
<i>Sarsia prolifera</i>	52	3	7	6	0		8	3	0	5		4	0	0	0	0	0	5	24	6		123
<i>Amphinema dinema</i>	0	6	0	0	0		0	0	0	0		0	0	0	0	0	0	0	0	0		6
<i>Amphinema rugosum</i>	0	0	0	0	0		0	0	0	0		2	0	0	0	0	0	0	0	0		2
<i>Halitiara formosa</i>	0	8	0	0	0		0	0	0	0		0	0	0	0	0	0	0	0	0		8
<i>Cubaia aprhrodite</i>	0	0	0	9	17		2	0	3	5		0	0	12	7	0	12	13	52	0		132
<i>Halocordyle disticha</i>	0	0	0	0	19		0	0	0	0		0	0	0	0	0	0	0	0	0		19
<i>Solmundella bitentaculata</i>	0	19	0	0	0		1	0	0	0		2	0	0	0	0	0	0	0	0		22
<i>Zanclus costata</i>	0	0	0	0	3		1	2	2	0		2	0	0	0	0	0	0	3	0		11
<i>Cunina octonaria</i>	0	0	0	0	0		2	0	0	0		0	0	0	0	0	0	0	0	0		2
<i>Rhopalonema velatum</i>	0	0	0	0	0		2	0	0	0		0	0	0	0	5	0	0	0	0		7
Total	290	298	7	33	44		61	140	3	15		154	92	47	13	5	12	18	226	6		1,464

1994, Suárez-Morales et al. 1995, Suárez-Morales et al. 1998). Only one species collected at Mahahual (*S. prolifera*) has not been recorded previously in the region. It has been reported from the northeastern Atlantic (Ranson 1925, Sanderson 1930, Russell 1938), and even from the Black Sea (Thiel 1935). This is the first record of this species in the northwestern Atlantic.

The number of species collected in this survey (17) is relatively low when compared with the medusa richness recorded in adjacent zones. Sixty-two species have been recorded from the Campeche Bank and the Mexican Caribbean (Phillips 1972, Segura-Puertas 1992, Segura-Puertas and Ordóñez-López 1994, Suárez-Morales et al. 1998). More than 20 species were found in a large embayment on the central portion of the Mexican Caribbean coast (Suárez-Morales et al. 1997).

The reef-related medusa fauna recorded off Belize by Larson (1982) can be compared with that recorded over Mahahual reef. Both belong to the same barrier reef system. Larson recorded 71 species in reef-related areas of Carrie Bow Cay, of which 80% were recorded in the fore-reef and 64% in the reef lagoon. The corresponding values for Mahahual were 88% at the fore-reef, 27% at the channel zone, and only 20% at the reef lagoon. It is

difficult to explain the differences in species richness with respect to Larson's (1982) results in a reef environment. To obtain most of the samples, he used a net with a 0.56 mm mesh opening, filtered an average of 250 m<sup>3</sup>, and made surface tows; his collections were made between 1730 and 1830. Up to this point, Larson's methods are similar to those we used at Mahahual. The main difference was probably related to material analyzed by Larson resulting from qualitative collections performed while diving, using light traps at night, and sampling with a beach seine and with dip nets. Medusa densities are commonly low in reef environments (Sammarco and Greenshaw 1984, Morales and Murillo 1996). The overall mean density recorded at Mahahual is similar (83 org./100 m<sup>3</sup>) to that recorded by Larson (1982) in plankton trawls from Carrie Bow (92.5 org./100 m<sup>3</sup>). However, there is no estimate on the species richness from plankton net collections. Larson (1982) recognized only 13 species as dominant; of this group, 8 are shared with the Mahahual community. In both cases, *L. tetraphylla*, *A. hemistoma*, *Solmundella bitentaculata*, and *C. aphrodite* were among the most abundant medusae. However, abundance of the dominant species in both systems showed several differences (Table 2). This suggests that although the number of species is almost

TABLE 2

The medusae collected in this survey at Mahahual and previously from the Campeche Bank, the Mexican Caribbean, and Belize. Key for citations in this table: 1. Larson (1982), 2. Phillips (1972), 3. Segura-Puertas (1992), 4. Segura-Puertas and Ordóñez-López (1994), 5. Zamponi et al. (1990), 6. Zamponi and Suárez-Morales (1991), 7. Suárez-Morales et al. (1995), and Suárez-Morales et al. (1997). \*Not previously recorded in the Caribbean Sea or Gulf of Mexico.

	Mahahual (this survey)	Campeche Bank (3, 4)	Mexican Caribbean (2, 5, 6, 7)	Belize (1)
<i>Amphinema dinema</i>	X	X		
<i>Amphinema rugosum</i>	X	X		X
<i>Zanclea costata</i>	X	X		
<i>Obelia</i> sp.	X	X		
<i>Clytia mcraayi</i>	X	X		
<i>Clytia folleata</i>	X		X	
<i>Solmundella bitentaculata</i>	X	X		X
<i>Liriope tetraphylla</i>	X	X	X	X
<i>Aglaura hemistoma</i>	X	X	X	X
<i>Rhopalonema velatum</i>	X	X		X
<i>Carybdea marsupialis</i>	X		X	X
<i>Podocoryne minima</i>	X	X		
<i>Sarsia prolifera</i> <sup>a</sup>	X			
<i>Halitiara formosa</i>	X	X		
<i>Cubaia aphrodite</i>	X			X
<i>Halocortyle disticha</i>	X			X
<i>Cunina octonaria</i>	X	X		X

TABLE 3

Density of the five dominant medusa species at two Caribbean reef environments.

	Mahahual (this survey)		Carrie Bow Cay (Larson 1982)	
	Relative density (%)	Density (org./100m <sup>2</sup> )	Relative density (%)	Density (org./100m <sup>2</sup> )
<i>Chytia mccradyi</i> + <i>C. folleata</i> (as <i>Phialucium</i> in Larson 1982)	4.1	35.5	32.0	28.0
<i>Solmundella bitentaculata</i>	1.3	1.04	1.5	1.2
<i>Liriope tetraphylla</i>	41.0	33.3	57.0	48.6
<i>Aglaura hemistoma</i>	22.0	18.0	3.3	2.9
<i>Cubaia aphrodite</i>	11.6	9.4	0.4	0.3

four times higher at Belize, the distribution of the species richness, the overall density, and the abundance of the dominant species are similar in the two surveys. This probably relates to the local abundance of *C. aphrodite* and of *A. hemistoma* at Mahahual; both were relatively scarce at Carrie Bow. *Aglaura hemistoma* is probably even more abundant in Mahahual during summer as recorded off the Caribbean (Suárez-Morales et al. 1998). Differences between the medusa fauna of Carrie Bow and Mahahual could be related to the physiographic features of each particular reef section.

In both areas, most of the remaining medusan species occurred in low numbers, which is a common feature of the medusa communities (Gili and Pagés 1987). The arrival of these oceanic species effects a local enrichment of species, but does not produce a major increase in the overall number of individuals. This pattern agrees with parallel results of Gili et al. (1988) from studies of cnidarian zooplankton in the western Mediterranean.

The nearshore hydrographic structure along the Caribbean coast of Mexico is related to the flow of a coastal countercurrent moving southward (Merino 1986) from the northernmost edge of the Caribbean coast. Its influence would explain, at least partially, the high affinity of the local medusa fauna with that of the Campeche Bank and the southern Gulf of Mexico (Phillips 1972, Segura-Puertas and Ordóñez-López 1994), and the relatively low affinity with the adjacent Belizean reef, which lies to the south (Larson 1982).

Segura-Puertas and Ordóñez-López (1994) reported 6 species (*A. hemistoma*, *L. tetraphylla*, *Nausithoe punctata*, *Rhopalonema velatum*, *Eutima gracilis* and *Z. costata*) as being the most common in the Campeche Bank and the oceanic Mexican Caribbean Sea. Our results

and those of Larson (1982) show that *L. tetraphylla* and *A. hemistoma* are also successful over reef environments (Table 3). *Aglaura hemistoma* has been reported as highly abundant in other tropical and subtropical environments (Gili and Pagés 1987, Gili et al. 1988). The seasonal (March-May) occurrence of the aggregating scyphozoan *Linuche unguiculata* seems to be a distinctive and dominant feature of the western Caribbean neritic and near oceanic environments (Larson 1982, Suárez-Morales et al. 1998). Reflecting its well-known seasonal behavior, this species was absent from our samples.

Communities of planktonic cnidarians are frequently dominated by a few of the most common species (Pugh and Boxshall 1984, Gili and Pagés 1987). Our results are similar. The most dominant medusae were distributed throughout the surveyed area; *L. tetraphylla*, *C. aphrodite*, and *A. hemistoma* were dominant in the three environments sampled. Uniformity in the distribution of planktonic cnidarian species is related to their high adaptability (Gili et al. 1988). This would explain, at least partially, the wide distribution of these medusae in the Mahahual reef area, and probably along the western Caribbean coasts. However, other groups, such as copepods, show a sharp difference in composition and a higher density within the reef lagoon than outside (Alvarez-Cadena et al. 1998).

In the Mexican Caribbean, a number of oceanic medusae reach neritic and even estuarine waters (Suárez-Morales et al. 1997, Suárez-Morales et al. 1998). This has been shown also for other zooplankton groups (Suárez-Morales and Gasca 1996). According to the results of Merino (1986) with drifting bottles, planktonic organisms transported northward by the western edge of the Yucatan Current tend to drift inshore. This would explain the

presence of oceanic medusae over the innermost portions of the narrow shelf. A relevant factor in the mesoscale distribution of zooplankton along the western Caribbean is the strong effect of tidal currents (Greer and Kjerfve 1982, Kjerfve 1982, Kjerfve et al. 1982) which bring an inflow of oceanic water to the lagoon through the channels and over the reef crests. This has been reported also for Mahahual (Castellanos and Suárez-Morales 1997). There is a strong import of oceanic fauna into the Mahahual reef area, as reflected in the dominance of oceanic forms and the high species richness over the fore-reef. This effect has been described also in the general reef zooplankton community at Carrie Bow Cay (Ferraris 1982).

The two assemblages defined by the Bray-Curtis Index showed a clear separation of the sampling stations in the surveyed area. The first, which comprised all the fore-reef stations, represents the primary influence of the oceanic fauna over the reef front. At this point, separation between the fore-reef and the reef lagoon seems to be sharp. However, the second group, which included the channel and reef lagoon stations, showed a secondary oceanic influence. This was represented mainly by the occurrence of the most common oceanic species in the area, a much lower species richness, and the occurrence of coastal species. Therefore, the main difference between the fore-reef and the reef lagoon medusa communities is the species richness, all areas being dominated by a few oceanic species. Migration and exchange of water into and out of the reef lagoon are seen to be relatively unimportant in determining the across-reef medusa community structure. This pattern is useful to describe the small-scale distribution of the medusae across the reef from day to day. Due to the expected uniformity of the zooplankton community along this reef system (Suárez-Morales and Rivera-Arriaga 1998), this pattern is probably valid along the entire reef system.

Apparently, the effect of the coastal countercurrent prevents the formation of a distinct seaward gradient of medusae, which is common in some other shelf-related areas studied (Pagés and Gili 1992). The occurrence of euryhaline medusae mixed with the oceanic ones has been reported also by Arai and Mason (1982) in the Strait of Georgia, and by Gili et al. (1988) in the Mediterranean.

From the known ecological affinities of the medusae recorded at Mahahual reef, three general groups can be recognized: 1) oceanic species (*L. tetraphylla*, *S. bitentaculata*, *A. hemistoma*, *R. velatum*, *N. punctata*, *Cyrtia tetrastyla*, and *Carybdea marsupialis*), which represented 60% of the medusa population; 2) neritic/coastal species (*A. dinema*, *A. rugosum*, *Obelia* sp., *C. folleata* and *Clytia maccradyi*), which accounted for 30%

of the medusae, and 3) coastal species (*P. minima*, *Zanclus costata*). The groups showed an overlapping distribution through the surveyed area.

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# AN ANNOTATED CHECKLIST AND KEY TO HERMIT CRABS OF TAMPA BAY, FLORIDA, AND SURROUNDING WATERS

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**ABSTRACT** Fourteen species of hermit crabs, belonging to 5 genera, were identified from 35 stations in Tampa Bay and adjacent continental shelf waters. Ninety-two samples were taken from the intertidal zone to 15 m with a variety of gear including dip nets, trawls, dredges, and hand collections using SCUBA. *Pagurus maclaughlinae*, *Pagurus longicarpus*, and *Pagurus pollicaris* were distributed throughout the bay. These species were often sympatric, and were commonly found in seagrass beds, sandy substrates, and sand/mud substrates, respectively. *Clibanarius vittatus*, *Pagurus gymnodactylus*, and *Pagurus stimpsoni* inhabited the higher salinity waters of the bay entrance. *Paguristes* sp., *Paguristes hummi*, *Pagurus impressus* and *Petrochirus diogenes* were collected from the lower bay to offshore on hard substrates and sand. *Paguristes puncticeps*, *Paguristes sericeus* and *Pagurus carolinensis* were collected only offshore on hard substrates. The latter species is reported from the Gulf of Mexico for the first time. *Isocheles wurdemanni* appears to be restricted to high energy beaches. An illustrated key as well as information on distribution, reproductive biology, taxonomic problems, symbionts, and coloration are presented.

## INTRODUCTION

Tampa Bay, the largest open-water estuary in Florida (Tampa Bay National Estuary Program 1996), supports a rich diversity of invertebrates which often occur in high densities (Simon 1974). However, the hermit crab fauna of this embayment and adjacent waters is poorly known. Although prior to the present study 15 species of hermit crabs were documented from the shallow waters (15 m or less) of the west coast of Florida, only 5 have been recorded from the Tampa Bay area (Table 1). The first species reported was *Pagurus pollicaris* Say, 1817, by Ives (1891) near the entrance of the Manatee River, which flows into Tampa Bay. Over 50 years later, *Paguristes hummi* Wass, 1955, was collected in tidal pools at the mouth of Tampa Bay. Provenzano (1959), in a major taxonomic paper on the shallow-water hermit crabs of Florida, cited only 1 species from the Tampa Bay area, *Pagurus longicarpus* Say, 1817. In the most recently published survey of macroinvertebrates of Tampa Bay, Dragovitch and Kelley (1964) found *Petrochirus diogenes* (Linnaeus, 1758) as well as *Pagurus longicarpus* and *P. pollicaris*. During the next 20 years, several systematic accounts were published on hermit crabs from Florida waters (McLaughlin and Provenzano 1974a, 1974b, McLaughlin 1975, García-Gómez 1982, Lemaitre 1982, Lemaitre et al. 1982), but they included no records from Tampa Bay. McLaughlin and Gore (1988) reported *P. maclaughlinae* García-Gómez, 1982 from Tampa Bay, in a study on the larval development of this species.

The present study was undertaken to assess the species composition and distribution of hermit crabs

inhabiting the Tampa Bay area, and provide an illustrated key as an aid to their identification. In addition, information on reproductive biology, coloration, and taxonomic considerations is included.

## MATERIALS AND METHODS

More than 90 samples (over 850 specimens) of hermit crabs were taken at 35 locations in the Tampa Bay, Florida, area to a depth of 15 m (Figure 1). Most collections were made by the authors from 1991-1997; however, additional material was examined from the University of Tampa Invertebrate Collection and the Florida Marine Research Institute, St. Petersburg, Florida. Specimens were collected with a variety of gear types and techniques; these are included in Appendix I with the station number (Figure 1), bottom type, temperature, salinity, depth, and species found at each station. Morphological terminology used for identification in the key is given in Figure 2. Unless otherwise noted, illustrations were prepared with the aid of a dissecting microscope and drawing tube.

Synonymies (restricted to primary taxonomic publications), material examined, distribution, and notes on ecological and reproductive biology are provided for each species in the systematic account. For species in which detailed coloration notes are available in the literature, only key color characters have been provided. For the other species listed below, descriptions of coloration for living specimens are reported for the first time, or additional detail is given to supplement existing notes. The material examined is presented in the following

manner: station number: date collected (number of specimens). Ovigerous females are designated with an (o). Collection dates followed by an asterisk indicate specimens borrowed from the Florida Marine Research Institute, St. Petersburg, Florida. Collections dates before 1991 that are not followed by an asterisk are from the University of Tampa Invertebrate Collection. Specimens collected during

the present study are deposited in the University of Tampa Invertebrate Collection except for representative specimens of each species which are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, (catalog number of specimens referred to as *Paguristes* sp. is USNM 265379).

TABLE 1

Hermit crab species reported from the west coast of Florida (Florida/Alabama border south to Cape Sable) to a depth of 15 m. Species records contained in this table were compiled from published literature as indicated. Lemaitre et al. (1982) concluded after a study of the species of the *Provenzano* Group, the distribution of *Pagurus annulipes* did not include the west coast of Florida. The authors did not examine Wass' (1955) material, and assigned his material to *Pagurus macLaughlinae*, *P. stimpsoni*, *P. gymnodactylus*, and/or *P. criniticornis*.

	Location	Reference
<b>Family Diogenidae:</b>		
<i>Clibanarius vittatus</i>	Pensacola St. Joseph Bay Sopchoppy Alligator Harbor Tampa Bay Little Gasparilla Pass	Cooley 1978 Brooks and Mariscal 1985a Hazlett 1981 Wass 1955 Present study Ives 1891
<i>Isocheles wurdemanni</i>	Perdido Key St. George Island Alligator Harbor Tampa Bay	Rakocinski et al. 1996 Caine 1978 Wass 1955; Provenzano 1959 Present Study
<i>Paguristes hummi</i>	Perdido Key Pensacola Dog Island Alligator Harbor Clearwater Beach Tampa Bay Sanibel Island Marco Island West Coast of Everglades	Rakocinski et al. 1996 Cooley 1978 Sandford 1995 Wass 1955; Wells 1969 Provenzano 1959 Wass 1955; Present study Gunter and Hall 1965 Provenzano 1959 Rouse 1970
<i>Paguristes puncticeps</i>	Northwest Coast of Florida off Tampa Bay	Provenzano 1959 Present study
<i>Paguristes sericeus</i>	off Horseshoe Cove off St. Petersburg Beach off Tampa Bay	Provenzano 1959 Provenzano 1959 Present study
<i>Paguristes tortugae</i>	Marco Island Everglades	Provenzano 1959; McLaughlin and Provenzano 1974a Rouse 1970
<i>Paguristes</i> sp.	Tampa Bay	Present study
<i>Petrochirus diogenes</i>	Pensacola Alligator Harbor Tampa Bay Everglades	Cooley 1978 Wass 1955 Dragovich and Kelley 1964; Present study Rouse 1970
<b>Family Paguridae:</b>		
<i>Pagurus annulipes</i> ?*	Alligator Harbor	Wass 1955
<i>Pagurus brevidactylus</i>	St. Andrews State Park	McLaughlin 1975
<i>Pagurus carolinensis</i>	off Tampa Bay	Present study

## HERMIT CRABS OF TAMPA BAY, FLORIDA

TABLE 1 (CONTINUED)

	Location	Reference
<b>Family Paguridae (continued):</b>		
<i>Pagurus gymnodactylus</i>	Perdido Key	Rakocinski et al. 1996
	Pensacola	Lemaitre 1982
	Cedar Key	Lemaitre 1982
	Anclote Anchorage	Lemaitre 1982
	Tampa Bay	Present study
	Marco Island	Lemaitre 1982
<i>Pagurus impressus</i>	Pensacola	Cooley 1978
	Dog Island	Sandford 1995
	Alligator Harbor	Wass 1955; Wells 1969
	Sea Horse Key	Provenzano 1959
	Clearwater Beach	Provenzano 1959
	Tampa Bay	Benedict 1892 (see Williams 1984); Present study
	Sanibel Island	Provenzano 1959
<i>Pagurus longicarpus</i>	Everglades	Rouse 1970
	Perdido Key	Rakocinski et al. 1996
	Pensacola	Cooley 1978
	St. Joseph Bay	Brooks and Mariscal 1985a
	Dog Island	Sandford 1995
	Alligator Harbor	Wass 1955; Wilber 1989
	Panacea	Wilber and Herrnkind 1982
	Wakulla Beach	Wilber and Herrnkind 1982, 1984; Wilber 1989
	Cedar Key	Provenzano 1959
	Crystal River	Lyons et al. 1971
	Clearwater Beach	Provenzano 1959
	Tampa Bay	Provenzano 1959; Dragovich & Kelley 1964; Present study
	Sanibel Island	Provenzano 1959; Gunter and Hall 1965
	Rookery Bay	Sheridan 1992
	Everglades	Rouse 1970
	Cape Sable	Tabb and Manning 1961
<i>Pagurus macLaughlinae</i>	Crystal River	García-Gómez 1982
	Anclote Anchorage	Lemaitre et al. 1982
	Tampa Bay	McLaughlin and Gore 1988; Present study
	Esterio Bay	García-Gómez 1982
	Rookery Bay	Sheridan 1992
	Everglades	García-Gómez 1982
<i>Pagurus pollicaris</i>	Pensacola	Cooley 1978
	St. Joseph Bay	Brooks and Mariscal 1985a, 1985b
	Dog Island	Sandford 1995
	Alligator Harbor	Wass 1955; Wells 1969
	Panacea	Brooks 1989
	Cedar Key	Provenzano 1959
	Tampa Bay	Ives 1891; Dragovich and Kelley 1964; Present study
	Lemon Bay	Provenzano 1959
	Little Gasparilla Pass	Provenzano 1959
	Charlotte Harbor	Provenzano 1959
	Sanibel Island	Provenzano 1959; Gunter and Hall 1965
	Rookery Bay	Sheridan 1992
	Everglades	Rouse 1970
<i>Pagurus stimpsoni</i>	Anclote Anchorage	Lemaitre et al. 1982
	Tampa Bay	Present study
<i>Iridopagurus caribbensis</i>	off Panama City	Williams 1984

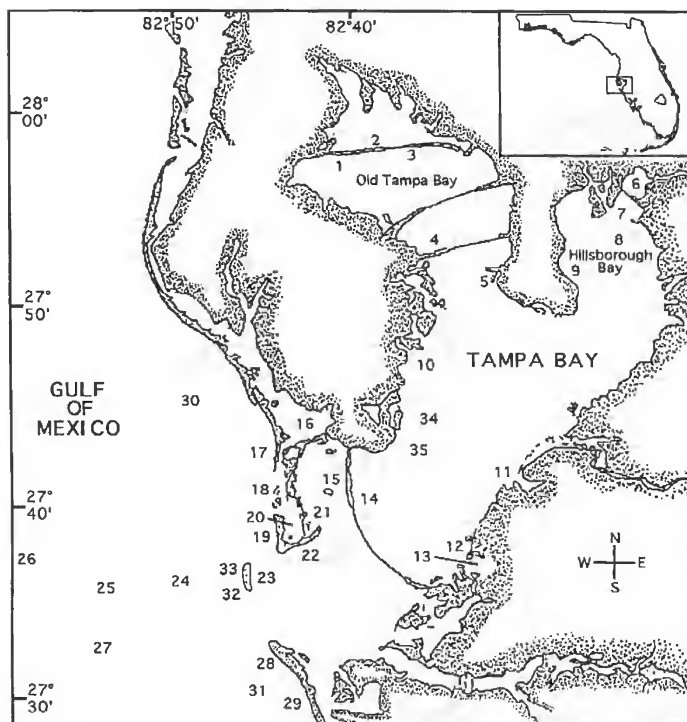


Figure 1. Location of collection sites in the Tampa Bay area.

#### Key to the Hermit Crabs of the Tampa Bay Area

1. Third maxillipeds approximated at base (Figure 3a) ..... [Family Diogenidae] 2  
     Third maxillipeds widely separated at base (Figure 3b) ..... [Family Paguridae] 8
2. No paired appendages present on first 2 abdominal segments of either sex; dactyl of fourth pereopod subterminal (Figure 3e) ..... 3  
     Paired appendages present on first 2 abdominal segments of male (Figure 3c), and first only of female (Figure 3d); dactyl of fourth pereopod terminal (Figure 3f) ..... 5
3. Chelipeds dissimilar and unequal, right slightly larger than left, right with calcareous tip (Figure 4a) ..... *Petrochirus diogenes*  
     Chelipeds similar and subequal, both with corneous tips (Figures 4b, c) ..... 4
4. Finger tips spooned (Figure 4b); antennal flagellum long and not setose ..... *Clibanarius vittatus*  
     Finger tips acuminate (Figure 4c); antennal flagellum short and very setose (Figure 4d) ..... *Isocheles wurdemanni*
5. Rostrum broadly rounded or pointed, not extending beyond lateral projections of cephalic shield (Figure 4e) ..... *Paguristes hummi*  
     Rostrum slender and clearly extending beyond level of lateral projections (Figures 4f, g, h) ..... 6
6. Ocular acicles ending in more than one terminal spine (Figure 4f) ..... *Paguristes* sp.  
     Ocular acicles ending in simple spine (Figures 4g, h) ..... 7
7. Anterior and lateral margins of cephalic shield meeting at broadly obtuse angle (Figure 4g) ..... *Paguristes puncticeps*  
     Anterior and lateral margins of cephalic shield meeting at near right angle (Figure 4h) ..... *Paguristes sericeus*
8. Ocular acicles ending in more than one spine or with submarginal spines (Figure 4i) ..... *Pagurus carolinensis*  
     Ocular acicles ending in a single terminal spine or with subterminal spine (Figure 4j) ..... 9

9. Antennal flagellum with paired setae, 3-8 articles in length, at least every second article proximally, decreasing in length distally (Figure 4k) .....

..... *Pagurus gymnodactylus*

Antennal flagellum with setae 1 article in length or less (Figure 4l), or irregularly short and long setae over entire length .....

10. One or both chelipeds broad, right chela dorsoventrally flattened (Figures 4m, n) .....

Both chelipeds narrow, right chela not dorsoventrally flattened (Figures 4o, p, q) .....

11. Dactyl of right cheliped with sharply produced angle on outer margin; lacking depression on dorsal surface of propodus of either cheliped (Figure 4m) .....

..... *Pagurus pollicaris*

Dactyl of right cheliped without sharply produced angle on outer margin; with depression on dorsal surface of propodus of both chelipeds (Figure 4n) .....

..... *Pagurus impressus*

12. Dactyls of 2nd and 3rd pereopods each without row of corneous spines on ventral margin (Figure 4r); eyestalks short, length approximately 3 times the width .....

..... *Pagurus longicarpus*

Dactyls of 2nd and 3rd pereopods armed with row of strong corneous spines on ventral margin (Figure 4s); eyestalks long, length at least 4 times the width .....

..... 13

13. Left chela with longitudinal ridge on dorsal surface of propodus, unarmed or with weak spines or tubercles (Figure 4p) .....

..... *Pagurus stimpsoni*

Left chela without ridge on dorsal surface of propodus, midline armed with a single or double row of strong spines (Figure 4q) .....

..... *Pagurus macLaughlinae*

## SYSTEMATIC ACCOUNT

### Family Diogenidae Ortmann, 1892

#### *Clibanarius vittatus* (Bosc, 1802)

*Pagurus vittatus*.—Bosc 1802:78, Plate 12, Figure 1.

*Clibanarius vittatus*.—Stimpson 1862:83.—Hay and Shore 1918:410, Plate 30, Figure 9.—Provenzano 1959:371, Figure 5D.—Holthuis 1959:141, Figures 26, 27.—Williams 1965:120, Figure 97.—Forest and de Saint Laurent 1967:104.—Coelho and Ramos 1972:170.—Felder 1973:32, Plate 3, Figure 20.—Williams 1984:194, Figure 135.—Abele and Kim 1986:29, 339d,e.

**Material.** Station 14: 3 Aug 1993(1).—Station 20:25 June 1993(1).—Station 23:May 1973(2).

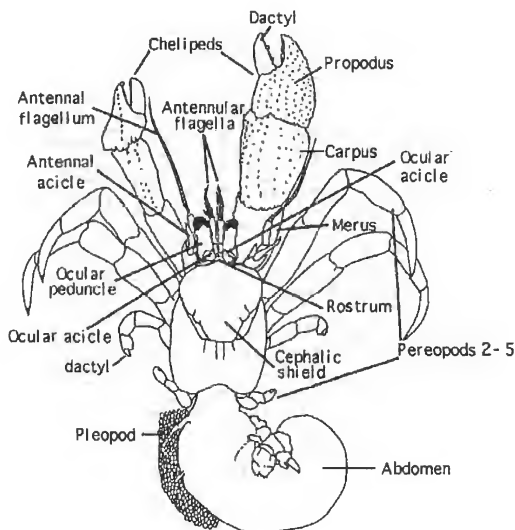


Figure 2. Schematic drawing of a hermit crab in dorsal view (after McLaughlin 1980)

**Known range.** Potomac River, Gunston, Virginia, to Florianopolis, Santa Catarina, Brazil (Forest and de Saint Laurent 1967).

**Remarks.** Only 4 specimens of *C. vittatus* were collected at the mouth of Tampa Bay in seagrass, sand/mud and rock jetty habitats. This species is commonly found in shallow subtidal and intertidal zones of harbor beaches, mud flats (Pearse et al. 1942), rock jetties, bay shores (Whitten et al. 1950), salt marshes near the ocean (Heard 1982), and seagrass-sand/mud areas (Lowery and Nelson 1988). Although *C. vittatus* is euryhaline (10-35‰) (Heard 1982), it is more commonly found at higher salinities, which may be necessary for egg development (Lowery and Nelson 1988). Although higher salinity habitats were sampled at different seasons in the present study, few animals were found. Thus, it appears that *C. vittatus* is uncommon in the Tampa Bay area.

Ovigerous females of *C. vittatus* were reported from North Carolina in June (Kircher 1967), South Carolina in July and August (Lang and Young 1977), east coast of Florida from April-September (Lowery and Nelson 1988), southern Florida in October (Provenzano 1959), northwestern Florida in June (Cooley 1978) and Texas from May-August (Fotheringham 1975). No ovigerous females were collected during this study.

**Coloration.** Light longitudinal stripes on the second and third pereopods. See Provenzano (1959) for additional detail.

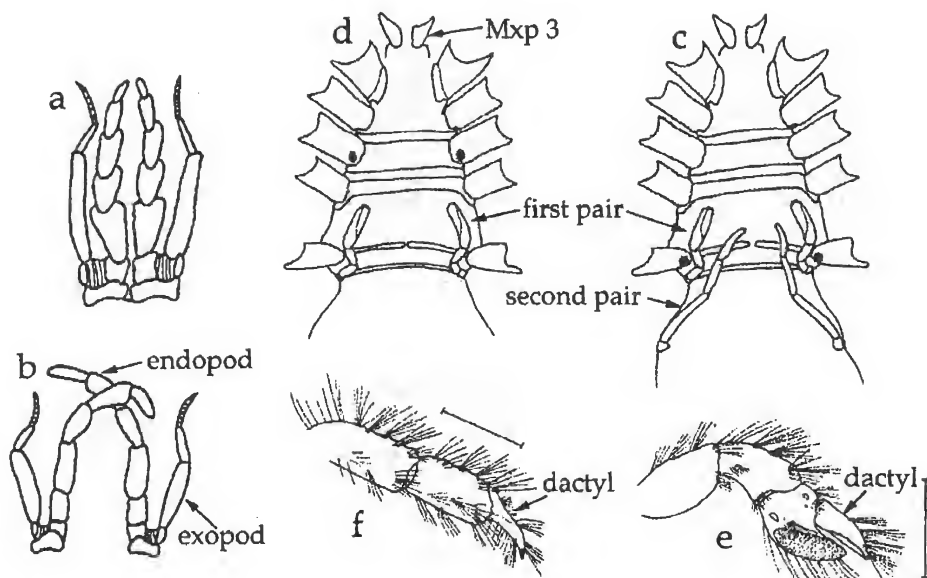


Figure 3. a) Third maxillipeds of Diogenidae, b) third maxillipeds of Paguridae (a and b redrawn from Provenzano 1961), c) *Paguristes*, ventral surface of male, gonopores on coxa of fifth pereopods, d) *Paguristes*, ventral surface of female, Mxp 3 = coxa of third maxilliped, gonopores on coxa of third pereopod, e) *Clibanarius vittatus*, distal end of fourth pereopod, dactyl subterminal (scale = 2.5 mm), f) *Paguristes sericeus*, distal end of fourth pereopod, dactyl terminal (scale = 2.5 mm).

*Isocheles wurdemanni* Stimpson, 1862

*Isocheles wurdemanni*—Stimpson 1862:85.—Provenzano 1959:375, Figure 7.—Felder, 1973:32, Plate 3, Figure 21.—Abele and Kim 1986:29, 353d.

**Material.** Station 28: 1 June 1991 (3).

**Known range.** Texas, Louisiana, west coast of Florida and Venezuela (Provenzano 1959).

**Remarks.** Whereas this species was only collected in shallow offshore waters along the high energy beaches of Anna Maria Island, it is probably found in similar habitats along the entire west coast of Florida. This is consistent with observations made by Caine (1978) who studied activities of *I. wurdemanni* along the Gulf of Mexico beaches of St. George Island, Florida. In his study, the majority of specimens were collected within 3 m of the splash zone or on the beach side of sand bars, 20–50 m offshore. Peak abundances were reported in the fall and spring with densities reaching 286 m<sup>-2</sup> along the offshore sand bars.

Ovigerous females of *I. wurdemanni* were reported from St. George Island, Florida, in the months of May, June, September, October and November (Caine 1978). No ovigerous females were collected in the present study.

**Coloration.** Body color white, see Stimpson (1859), Wass (1955), and Provenzano (1959) for additional detail.

*Petrochirus diogenes* (Linnaeus, 1758)

*Cancer diogenes*—Linnaeus 1758:631.

*Cancer bahamensis*—Herbst 1796:30.

*Petrochirus granulatus*—Stimpson 1859:234.

*Petrochirus bahamensis*—Benedict 1901:140.—Hay and Shore 1918:410, Plate 30, Figure 6.—Schmitt 1935:206, Figure 66.—Provenzano 1959:378, Figure 8.—Provenzano 1961:153.

*Petrochirus diogenes*—Holthuis 1959:151.—Williams 1965:122, Figure 98.—Provenzano 1968:147, Figures. 1–12.—Felder 1973:30, Plate 3, Figure 14.—Williams 1984:198, Figure 138.—Abele and Kim 1986:31, 353e,f.

**Material.** Station 10: 28 May 1966\* (1).—Station 14: 23 Jan. 1993 (1).—Station 23: 9 Feb. 1965\* (1).—Station 26: 8 May 1983 (3), 24 Oct. 1992 (1).—Station 27: May 1978 (1), 30 Aug. 1980 (1).—Station 30: 2 Oct. 1993 (1).

**Known range.** Off Cape Lookout, North Carolina, through Gulf of Mexico and West Indies south to off Ilha de São Sebastiao, Brazil, 23°42.5'S, 45°14.5'W (Forest and de Saint Laurent, 1967).

**Remarks.** *Petrochirus diogenes* is rare in shallow waters of the Tampa Bay area. Most specimens were collected on sand near hard substrates at the mouth of Tampa Bay or in offshore waters. This species has been reported on mud, mud/shell and sand bottoms in

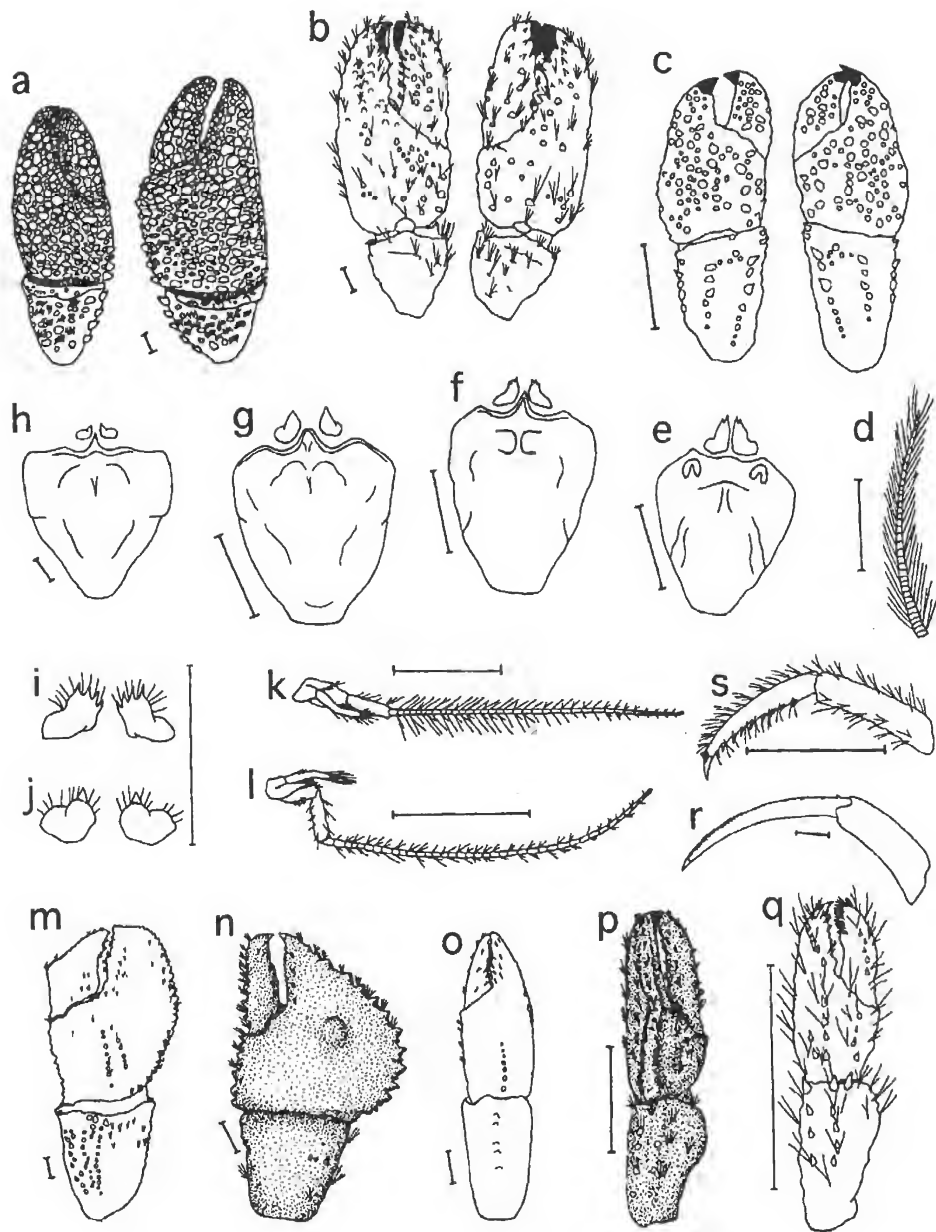


Figure 4. Hermit crabs of the Tampa Bay area. a) Chelipeds of *Petrochirus diogenes*, b) chelipeds of *Clibanarius vittatus*, c) chelipeds of *Isocheles wurdemannii*, d) antennal flagellum of *Isocheles wurdemannii*, e) cephalic shield and ocular acicles of *Paguristes hummi*, f) cephalic shield and ocular acicles of *Paguristes* sp., g) cephalic shield and ocular acicles of *Paguristes puncticeps*, h) cephalic shield and ocular acicles of *Paguristes sericeus*, i) ocular acicles of *Pagurus carolinensis*, j) ocular acicles of *Pagurus maclaughlinae*, k) antennal peduncle of *Pagurus gymniodactylus*, l) antennal peduncle of *Pagurus maclaughlinae*, m) right cheliped of *Pagurus pollicaris*, n) right cheliped of *Pagurus impressus*, o) right cheliped of *Pagurus longicarpus*, p) left cheliped of *Pagurus stimpsoni*, q) left cheliped of *Pagurus maclaughlinae*, r) dactyl and propodus of second pereopod of *Pagurus longicarpus*, s) dactyl and propodus of second pereopod of *Pagurus maclaughlinae*. Scales equal 2 mm for k and l and 1 mm for all other illustrations.



continental shelf waters on the Tortugas shrimping grounds (Provenzano 1959), off Mississippi (Franks et al. 1972), on brown shrimp grounds in the western Gulf of Mexico (Hildebrand 1954), and has been found as deep as 128 m (Wenner and Read 1982). It may be fairly common in deeper continental shelf waters off Tampa Bay.

Ovigerous females were reported in June from Texas, in August from west Florida (Provenzano 1968), and in March from the Virgin Islands (Provenzano 1961). No ovigerous females were found during this study.

**Coloration.** Body color generally reddish with color fading at joints. Antennal flagellum with red and white bands; cornea blue and black. See Provenzano (1959) for additional detail.

#### *Paguristes hummi* Wass, 1955

*Paguristes hummi*—Wass 1955:148, Figures 1-4.—Provenzano 1959:381, Figure 9.—Felder 1973:31, Plate 3, Figure 16.—Williams 1984:200, Figure 139.—Abele and Kim 1986:30, 343a.—Campos and Sánchez 1995:576, Figure 7.

**Material.** Station 13: 26 Sept. 1992 (1).—Station 14: 13 June 1993 (1).—Station 16: 12 Oct. 1983 (1).—Station 18: 2 Oct. 1993 (3).—Station 24: 3 Jan. 1966\* (1).—Station 25: 31 May 1966\* (1).—Station 27: 1 Sept. 1991 (1).—Station 28: 1 June 1991 (4), 1 Oct. 1991 (1).—Station 30: 2 Oct. 1993 (1), 29 April 1994 (4).—Station 31: 26 July 1995 (4, 1o).

**Known range.** Newport River, North Carolina, to Sapelo Island, Georgia; Marco Island, southwestern Florida, to off Isles Dernieres, Louisiana (Williams 1984); Caribbean coast of Colombia (Campos and Sánchez 1995).

**Remarks.** *Paguristes hummi* was found both offshore and in lower Tampa Bay, usually associated with hard substrates. Wass (1955) reported *P. hummi* inhabiting a variety of gastropod shells in the intertidal zone only on the south side of Mullet Key at the mouth of Tampa Bay where it was abundant at times. This species was found in shelly areas of Beaufort, North Carolina, but was more abundant offshore on rocky outcrops (Kellogg 1971). In the Alligator Harbor-Dog Island area of northwest Florida, *P. hummi* has been found to inhabit sponges (Wass 1955, Wells 1969, Sandford 1995), which have been identified as the hermit crab sponge *Spongosorites suberitoides* (Sandford and Kelley-Borges 1997). All specimens collected in the present study were found in gastropod shells.

Ovigerous females of *P. hummi* were reported from northwestern Florida in January and July (Cooley 1978), and from southwestern Florida in February (Provenzano 1959), October, and November (Rouse 1970). The only ovigerous female collected in this study was taken in July.

**Coloration.** Body color generally white. Striking blue color mark, ringed by black and yellow, present on the

inner surface of the merus of both chelipeds. See Wass (1955) and Provenzano (1959) for additional detail.

#### *Paguristes puncticeps* Benedict, 1901

*Paguristes puncticeps*—Benedict 1901:144, Plate 4, Figure 4, Plate 5, Figure 2.—Provenzano 1959:384, Figure 10a.—Abele and Kim 1986:30, 347e.—Campos and Sánchez 1995:572, Figure 2.

**Material.** Station 25: 31 Dec. 1966\* (1).—Station 26: 8 May 1983 (1), 4 Oct. 1992 (1), 19 April 1997 (1, 1o).—Station 27: 1 May 1978 (1), Oct. 1981 (1), 1 Sept. 1991 (2).—Station 30: 2 Oct. 1993 (4).

**Known range.** Northwestern Florida; south Florida to Jamaica, probably throughout the West Indies (Provenzano 1959); Caribbean coast of Columbia (Campos and Sánchez 1995); off Tampa Bay, Florida (present study).

**Remarks.** This report of *P. puncticeps* is the first from a locality that occurs between northwestern Florida and Miami and is indicative of a probable continuous distribution of the species along the west coast of Florida and throughout the Caribbean Sea. This species was only found offshore of Tampa Bay in association with hard substrates in depths of 10-15 m. *Paguristes puncticeps* has been collected as deep as 19 m from the Tortugas shrimp grounds (Provenzano 1959). One ovigerous female was collected in April during the present study, and one was reported from Cuba in January (Provenzano 1959).

*Paguristes sericeus* and *P. puncticeps* are morphologically similar species and were collected together in continental shelf waters off Tampa Bay. Some confusion exists in the literature concerning the length of the antennal peduncles in relation to the antennal acicles for these 2 species. All illustrations except Figures 93a and 142a of Williams (1965, 1984), respectively, show the relationship of these characters to be similar in both species: the antennal peduncle is slightly longer than the antennal acicle (Milne Edwards and Bouvier 1893, Benedict 1901, Provenzano 1959). The relationship of these characters is not mentioned in descriptions of either species (Milne Edwards 1880, Milne Edwards and Bouvier 1893, Benedict 1901, Provenzano 1959), with the exception of Williams (1965, 1984) who states correctly, "Antennal peduncles slightly exceeding acicles." However, an error exists in Figure 93a (Williams 1965, reproduced as Figure 142a in Williams 1984). In these figures the antennal peduncle of *P. sericeus* is shown to be considerably shorter than the antennal acicle. Abele and Kim (1986) used this inaccurate illustration along with a probable misinterpretation of the word "acicle" in the passage above as a basis for separating *P. sericeus* and *P.*

*puncticeps*. They appear to have interpreted Williams' use of "acicle" to mean ocular acicle, whereas he was instead referring to the antennal acicle in that section. Using this interpretation and Williams' illustration, *P. puncticeps* appears to have a much longer antennal peduncle in relation to the ocular acicle than does *P. sericeus*. However, since the relationships among the lengths of the antennal peduncle, antennal acicle and ocular acicle are similar for both species, these characters cannot be used to distinguish them.

As indicated in couplet 7 of the key and Figures 4g,h of the present study, the shape of the antero-lateral margins of the cephalic shield appears to be the most reliable character which separates *P. sericeus* from *P. puncticeps*. Provenzano (1959) discussed the contrast between the sloping angles of the shield in *P. puncticeps*, and the near right angles found in *P. sericeus* (= *P. rectifrons* sensu Provenzano). The presence of white spots on the ocular peduncles of fresh *P. puncticeps* is also mentioned by Provenzano as a differentiating characteristic. However, this color pattern is not always present in live material and should be used with caution.

**Coloration.** Body color red with white spots. At times, juveniles bright red and adults rust red. Ocular peduncles reddish orange, usually with white spots; cornea bright blue. Antennular and antennal flagella reddish. Proximal and distal ends of each segment lighter in color than middle on all walking legs; setae fringing dorsal and ventral areas occasionally green from accumulation of algae. See Provenzano (1959) for additional coloration notes.

#### *Paguristes sericeus* Milne Edwards, 1880

*Paguristes sericeus*—Milne Edwards 1880:44.—Milne Edwards and Bouvier 1893:46, Plate 3, Figures 14-22.—Provenzano 1961:155.—Williams 1965:117, Figure 93.—Provenzano and Rice 1966: 54, Figures 1-10.—Felder 1973:32, Plate 3, Figure 19.—Pequegnat and Ray 1974:242, Figure 44.—Williams 1984:203, Figure 142.—Abele and Kim 1986:30, 347c,d.

*Paguristes tenuirostris*—Benedict 1901:143, Plate 4, Figure 1.

*Paguristes rectifrons*—Benedict 1901:145, Plate 4, Figure 7.

**Material.** Station 26: 8 May 1983 (3), 30 Apr. 1995 (2).—Station 27: 1 Sept. 1991 (1).

**Known range.** Off Cape Lookout, North Carolina; West Flower Garden Bank, northwest Gulf of Mexico to the Virgin Islands (Williams 1984).

**Remarks.** This species was collected only offshore of Tampa Bay on sand near limestone outcroppings at a depth of 15 m. *Paguristes sericeus* has been found on sand and coral rubble (Provenzano 1961) at depths of 9 to 145 m (Williams 1984).

Ovigerous females were reported from off St. Petersburg Beach, Florida, in July (Provenzano 1959), on the Dry Tortugas shrimping grounds in March and May (Provenzano 1959, Rice and Provenzano 1965), and in the Virgin Islands in March and April (Provenzano 1961). No ovigerous females were collected during the present study.

For taxonomic considerations see remarks under *P. puncticeps*.

**Coloration.** Similar to *P. puncticeps*, except overall color generally more orange-red, and eyestalks without white spotting. See Provenzano (1959, 1961), Provenzano and Rice (1966), and Williams (1984) for additional coloration notes.

#### *Paguristes* sp.

**Material.** Station 13: 2 Mar. 1991 (1), 26 Sept. 1992 (6).—Station 14: Apr. 1979 (1), 18 June 1992 (1, 3o), 3 Aug. 1993 (1).—Station 26: 24 Oct. 1992 (3), 19 Apr. 1997 (1).—Station 27: 1 Sept. 1991 (7).—Station 29: 12 Oct. 1991 (2).—Station 30: 2 Oct. 1993 (3).—Station 31: 26 July 1995 (3, 1o).—Station 33: 29 Sept. 1996 (3, 1o).

**Remarks.** These specimens appear to be of an undescribed species most similar to *Paguristes tortugae* Schmitt, 1933. The most obvious differences occur in the color patterns. *Paguristes tortugae* has reddish-purple, transverse bands on the pereopods whereas our specimens are unbanded with a brownish-green body color (see coloration section). Future work with these species should yield additional characters for their distinction.

*Paguristes* sp. is relatively common in lower Tampa Bay, especially near Bishop Harbor (station 13) where it was often found in large groups on or near basket sponges. It was rarely taken offshore, but was found near hard substrates in all collections. Ovigerous females were found in the summer and fall.

**Coloration.** Cephalic shield green or brownish-green with yellowish-orange and white spots; posterior part of thorax pinkish with irregular red spots and occasionally blue patches laterally; area postero-medial to cephalic shield yellowish-orange with green and white patches; posterior border of carapace red. Proximal one-fourth of ocular peduncles brown or greenish-brown, distal part white, circumscribed with one proximal orangish-yellow and one distal dark brown band; cornea black. Proximal

half of ocular acicles brown, distal half white. Antennular peduncles marked with 3 brown or brownish-green and white bands; flagella brown. Antennal peduncles brown with white spines, distal segments circumscribed with 2 brown and 2 white bands; flagella colorless, every other article white distally, middle part of each article solid brown or with brown streaks laterally. Third maxillipeds with brown and white bands. Chelipeds with dactyls and fixed fingers yellowish, proximal part of propodi and remaining segments greenish-brown; proximal one-half of dactyls and three-fourths of propodi with reddish, white-tipped tubercles or spines; spines on dorsomesial margins of propodi and carpus reddish proximally, followed by yellow rings and brown tips; merus with yellowish reticulations and white dots mesially and laterally, and reddish-orange patches along dorsal margin. Pereopods generally greenish-brown with white or bluish-white spots and reticulations; dactyls with brown spines, other articles with reddish, white-tipped spines; carpi with dorsal one-half reddish proximally. Abdomen yellowish with red patches and white spots; transverse blue streaks laterally.

#### Family Paguridae Latreille, 1803

##### *Pagurus carolinensis* McLaughlin, 1975

*Pagurus* near *bonairensis*—Pearse and Williams 1951:143.

*Pagurus brevidactylus*—Provenzano 1959:413, Figure 20.—Williams 1965:132, Figure 107.

*Pagurus carolinensis*—McLaughlin 1975:365, Figures 4-6.—Lemaitre et al. 1982:677.—Williams 1984:212, Figure 150.—Abele and Kim 1986:33, 375f,g.

**Material.** Station 26: 24 Oct. 1992 (1), 4 Mar. 1997 (1).—Station 27: Oct. 1991 (1).—Station 30: 2 Oct. 1993 (3).—31: 26 July 1995 (2).

**Known range.** Off Newport River (Kellogg 1971) and Cape Lookout, North Carolina, to southeastern Florida (Williams 1984); off Tampa Bay, Florida (present study).

**Remarks.** This is the first record of *P. carolinensis* in the Gulf of Mexico. Only 6 specimens were collected offshore in association with hard substrates at depths of 5-15 m. This species has been reported to prefer hard bottom in areas of good water circulation (Provenzano 1959) at depths of 2 to 53 m (Lemaitre et al. 1982).

Ovigerous females were reported in June, July, and August from North Carolina, November, July-October in Georgia and March-August in Florida (Williams 1984). No ovigerous females were collected in the present study.

*Pagurus carolinensis*, reported from the Gulf of Mexico for the first time in the present study, is morphologically very similar to *P. brevidactylus*. Although

this latter species was not found in the Tampa Bay area, it occurs in northwest Florida. Future studies may document an overlap in the ranges of these 2 species in the Gulf of Mexico similar to their overlap in southeast Florida (Lemaitre et al. 1982). The spination of the left chelae may be used to separate these 2 species. *Pagurus brevidactylus* (Stimpson, 1859) has a longitudinal row of strong or moderately strong spines near the dorsolateral margin of the propodus, while *P. carolinensis* may have small or no spines in this area. In addition, *P. brevidactylus* has shorter setae on the articles of the antennal flagella and longer, more slender ocular peduncles than *P. carolinensis*. Coloration may be used to separate live specimens of these species. *Pagurus brevidactylus* has dark green to brownish black continuous stripes on the pereopods, and striped chelipeds. *Pagurus carolinensis* has rust red to maroon stripes on the pereopods that do not extend to the distal and proximal margins of each segment, and the chelipeds are not striped (Lemaitre et al. 1982).

**Coloration.** See remarks above. Additional coloration notes are found in Provenzano [1959 (= *P. brevidactylus*)].

##### *Pagurus gymnodactylus* Lemaitre, 1982

*Pagurus annulipes*—Felder 1973:26, Plate 3, Figure 4 [not *P. annulipes* (Stimpson)].—Williams 1974:41.

*Pagurus gymnodactylus*—Lemaitre 1982:657, Figures 1, 2, 4c, d, 5a, b.—Lemaitre et al. 1982:687.—Abele and Kim 1986:33, 377h,i,j.

**Material.** Station 14: 3 Aug. 1993 (4).—Station 18: 2 Oct. 1993 (8, 10).—Station 32: 26 July 1995 (1).

**Known range.** Gulf of Mexico from Mexico to west coast of Florida (Lemaitre et al. 1982).

**Remarks.** *Pagurus gymnodactylus* was collected on sand and hard substrates in shallow subtidal depths at the mouth of Tampa Bay. This species has been found from the subtidal zone to 19 m (Lemaitre et al. 1982).

No information is available on the reproduction of this species. However, in the present study, one ovigerous female was found in October.

**Coloration.** While some specimens appeared to be almost completely white, those with color displayed the following characteristics: carapace mottled yellow-brown, occasionally with green and red splotches, red flecks laterally. Abdomen transparent blue. Ocular acicles, eyestalks, and antennular flagella transparent with red and white flecks; eyestalks sometimes with central, horizontal, blue-green band. Antennal flagella transparent, marked with white every 2-5 articles; peduncle transparent with red and white flecks. First and second maxillipeds

mottled red and white at bases. Third maxillipeds with blue to red transverse bands. Merus, carpus and propodus of right cheliped mottled brown, distal part of propodus and dactyl white. Dactyls, propodi, carpi, and meri of second and third pereopods with mottled brown transverse bands.

*Pagurus impressus* (Benedict, 1892)

*Eupagurus impressus*—Benedict 1892:5.

*Pagurus impressus*—Provenzano 1959:399, Figure 15.—Williams 1965:129, Figure 104.—Felder 1973:27, Plate 3, Figure 9.—Williams 1984:215, Figure 153.—Abele and Kim 1986:33, 377a,b,c.

**Material.** Station 13: 26 Sept 1992 (4).—Station 14: Apr. 1982 (3), May 1983 (1), 23 Jan. 1993 (25+), 3 Aug. 1993 (25+), 11 Sept. 1993 (2).—Station 15: May 1983 (2).—Station 16: 12 Oct. 1983 (1).—Station 19: 19 Feb. 1982 (2), 25 June 1993 (1).—Station 28: 1 Oct. 1990 (2).—Station 29: 12 Oct. 1991 (25+).—Station 30: 2 Oct. 1993 (6), 29 April 1994 (2).—Station 31: 26 July 1995 (9).

**Known range.** North Carolina to Cape Canaveral, Florida; Florida Bay north to Pensacola, Florida; Port Aransas, Texas (Williams 1984); Padre Island, Texas (Felder 1973).

**Remarks.** This species is very common at the mouth of Tampa Bay and in shallow offshore waters. It was often found in congregations on sand near hard substrates. *Pagurus impressus* has been reported to inhabit areas of sand, seagrass beds or pilings, and has been found in hermit crab sponges (Wass 1955, Wells 1969, Sandford 1995). In the Dog Island area, *P. impressus* has been shown to move into the intertidal zone close to the shoreline in January, with many individuals inhabiting the hermit crab sponge *S. suberitoides* (Sandford and Kelley-Borges 1997).

Ovigerous females were collected from the Carolinas and Georgia in January and February, and in Florida in February and April (Williams 1984). In the present study, ovigerous females were collected in January only.

**Coloration.** Eyestalks dark brown with white specks on dorsal surface, red at base, and longitudinal blue stripe on ventral surface. Cornea black with translucent yellow covering. Antennal and antennular flagella yellow, sometimes red at base. Cephalic shield mottled yellow and brown. Thorax generally reddish-brown with white spots; laterally, darker red with white spots. Third maxillipeds brown with white spots, white at joints. First and second maxillipeds reddish with white spots. Propodi and dactyls of chelipeds almost solid brownish-orange to rust-red on dorsal surface, sometimes with small white spots, ventral surface darker brown with white spots; carpi and meri mottled dark brown with white transverse bands. Dactyls of second and third pereopods mottled brownish orange,

with thin longitudinal stripe on lateral and mesial faces; propodi, carpus and meri mottled brown, with white transverse bands near joints. Joint between carpus and merus of all walking legs reddish in color. See Provenzano (1959) for additional coloration notes.

*Pagurus longicarpus* Say, 1817

*Pagurus longicarpus*—Say 1817:163.—Hay and Shore 1918:411.—Provenzano 1959:394, Figure 13.—Williams 1965:125, Figure 101.—Felder 1973:27, Plate 3, Figure 7.—Williams 1984:216, Figure 154.—Abele and Kim 1986:33, 381c,d,e.

**Material.** Station 1: May 1986 (18), 5 Feb. 1991 (24), 13 Jan., 1992 (2), 23 June 1992 (10), 1 Sept. 1992 (12), 21 Jan. 1993 (5), 29 Nov. 1993 (6).—Station 2: 5 May 1977 (7).—Station 3: 1 Feb. 1992 (4), 5 May 1992 (5), 18 June 1992 (10), 19 Sept. 1992 (6), 13 Jan. 1993, 11 May 1993 (6, 10).—Station 4: 11 Nov. 1991 (2), 4 Jan. 1993 (4).—Station 5: 26 Sept. 1976 (1), 28 Sept. 1976 (2), Sept. 1991 (3), 16 Jan. 1993 (3), 11 May 1993 (9).—Station 6: 8 June 1978 (12).—Station 9: 18 Sept. 1992 (2), 6 Jan. 1993 (1), May 1993 (3).—Station 12: 7 May 1983 (1).—Station 14: Oct. 1979 (6), 3 Aug. 1993 (6), 11 Sept. 1993 (4).—Station 17: 31 Dec. 1964\* (1).—Station 18: 11 Dec. 1965\* (8).—Station 19: 2 Nov. 1991 (7).—Station 20: 8 Jan. 1965\* (4).—Station 21: 9 Feb. 1965\* (1).—Station 22: 25 June 1993.

**Known range.** Minas Basin and Chignecto Bay, Nova Scotia (Bousfield and Liem 1960) to Hutchinson Island, Florida (Camp et al. 1977); southwestern Florida to the coast of Texas (Whitten et al. 1950, Provenzano 1959, Rouse 1970).

**Remarks.** *Pagurus longicarpus* is commonly found on sand, sand/mud, grass, and hard substrate habitats throughout the intertidal and shallow subtidal waters of the entire Tampa Bay area. This species has been reported from harbor beaches and channels on a variety of substrates (Williams 1984), from the intertidal to 200 m (Wenner and Boesch 1979). Its ubiquity in bays and estuaries prevents its use in distinguishing shallow water habitats (Allee 1923).

Ovigerous females of *P. longicarpus* were collected from April–September in Massachusetts (Carlson and Ebersole 1995), February–September in North Carolina, March–July in Georgia (Williams 1984), September–April in Florida (Wass 1955, Dragovich and Kelley 1964, Lyons et al. 1971), and winter in Texas (Fotheringham 1975). In the present study, ovigerous females were collected in May.

**Coloration.** Abdomen and thorax brown, sometimes with white spots on cephalic shield. Ocular acicles white, eyestalks white with brown near black corneas. Antennular

peduncles brown and white; flagella white. Antennal peduncles and acicles brown; flagella brown with white article every 2-4 articles. Maxillipeds brown proximally. Right cheliped white or off-white, with 3 longitudinal brown, rust or yellowish-brown stripes; stripes joined at merus, then separated distally on mesial, dorsal, and lateral margins. Second and third pereopods with longitudinal stripe on lateral and mesial faces. See Provenzano (1959) for additional coloration notes.

***Pagurus maclaughlinae* García-Gómez, 1982**

?*Eupagurus annulipes*—Ives 1891:193. [not *E. annulipes* Stimpson].

*Pagurus annulipes*—Schmitt 1935:205 (in part).—Provenzano 1959:407, Figure 18 [not *P. annulipes* (Stimpson)].—Williams 1965:130 (in part), Figure 105.—Forest and de Saint Laurent 1967:127 (in part).

*Pagurus bonairensis*—Felder 1973:26 (in part), Plate 3, Figure 5. [not *P. bonairensis* Schmitt].

*Pagurus maclaughlinae*—García-Gómez 1982:647, Figures 1, 2.—Lemaitre et al. 1982:691.—Abele and Kim 1986:33, 377d,e,f.

**Material.** Station 1: 13 Jan. 1992 (1), 21 Jan. 1993 (25+).—Station 3: 28 Jan. 1992 (25+), 1 Feb. 1992 (1), 28 Feb. 1992 (25+), 5 May 1992 (25+), 18 June 1992 (1), 13 Jan. 1993 (25+), 11 May 1993 (25+).—Station 5: 18 Sept. 1992 (25+), 16 Jan. 1993 (25+), 11 May 1993 (25+).—Station 9: 6 Jan. 1993 (3).—Station 11: 2 Oct. 1992 (25+), 16 Jan. 1993 (25+), 12 May 1993 (25+), 17 July 1993 (25+).—Station 13: 26 Sept. 1992 (5).—Station 14: 23 Jan. 1993 (25+), 3 Aug. 1993 (25+), 11 Sept. 1993 (25+).—Station 15: 1 June 1991 (5).—Station 20: 25 June 1993 (15).—Station 28: 1 June 1991 (3).—Station 34: 15 Apr. 1995 (4, 1).—Station 35: 28 Apr. 1996 (3, 1).

**Known range.** Wassaw Sound, Georgia, to Puerto Rico; northern Gulf of Mexico to Florida Keys (García-Gómez 1982, Lemaitre et al. 1982).

**Remarks.** *Pagurus maclaughlinae* is one of the most common species found in the shallow subtidal waters of Tampa Bay. Although this species is typically found in seagrass beds, specimens have also been collected on hard substrates and high energy beaches. At Station 14, individuals were found clinging to the gorgonian *Leptogorgia virgulata*. *Pagurus maclaughlinae* has been reported at depths of 1-5 m (Lemaitre et al. 1982).

Ovigerous females were collected each month of the year in Indian River Lagoon, on the Atlantic Coast of Florida, with peaks (> 50%) occurring in August-October and February-June (Tunberg et al. 1994). In Tampa Bay, *P. maclaughlinae* appears to reproduce throughout the

year since ovigerous females were found during each season.

**Coloration.** Antennal flagellum with blue and white transverse bands. Pereopods with brown and white transverse bands. Chelipeds light brown with white tubercles, distal ends of dactyl and fixed finger white. See García-Gómez (1982) for additional detail.

***Pagurus pollicaris* Say, 1817**

*Pagurus pollicaris*—Say 1817:162.—Hay and Shore 1918:411, Plate 30, Figure 1.—Provenzano 1959:401, Figure 16.—Williams 1965:128, Figure 103.—Felder 1973:27, Plate 3, Figure 8.—Williams 1984:220, Figure 157.—Abele and Kim 1986:33, 375h,i.

**Material.** Station 1: 13 Jan. 1992 (1), 1 Sept. 1992 (2).—Station 3: 11 May 1993 (1).—Station 4: 3 July 1992 (3), 4 Jan. 1993 (4).—Station 5: 26 Sept. 1976 (1), 28 Sept. 1976 (1), Sept. 1991 (1), 11 May 1993 (1).—Station 7: 10 Dec. 1982 (1).—Station 8: 4 Jan. 1974 (1).—Station 9: 18 Sept. 1992 (3), 6 Jan. 1993 (1), 11 May 1993 (2).—Station 12: 7 May 1983 (1).—Station 13: 7 May 1983 (1), Apr. 1991 (1), 26 Sept. 1992 (2).—Station 14: 14 Apr. 1970 (1), April 1979 (4), Oct. 1979 (1), 3 Aug. 1993 (3), 11 Sept. 1993 (3).—Station 15: Apr. 1979 (3).—Station 19: 1 Feb. 1992 (3).—Station 30: Oct. 1993 (2).—Station 33: 29 Sept. 1996 (1).—Station 34: 15 Apr. 1995 (2).—Station 35: 28 Apr. 1996 (2).

**Known range.** Grand Manan, New Brunswick, to northeastern Florida; Key West, Florida, to Texas (Provenzano 1959, Williams 1984).

**Remarks.** *Pagurus pollicaris* was collected throughout Tampa Bay, was usually found alone on sand in the shallow subtidal zone, and was occasionally near hard substrates. This species is known to inhabit shallow estuaries, deep harbor channels, and littoral waters (Williams 1984), although it has been collected to a depth of 112 m (Wenner and Boesch 1979).

Ovigerous females were collected from early spring to June in Massachusetts (Nyblade 1970, Carlon and Ebersole 1995), January and February in North Carolina, and in the winter in Texas (Fotheringham 1975). Ovigerous females were taken from northwestern Florida in February (Cooley 1978), near Crystal River in December (Lyons et al. 1971), in Tampa Bay in November and December (Dragovich and Kelley 1964), and in southwestern Florida in March (Provenzano 1959). No ovigerous females were collected during this study.

**Coloration.** Eyestalks white with dark brown surrounding cornea on dorsal part, light yellow near cornea; cornea light blue-grey with black ring. Antennular peduncles tan to green; flagella mostly drab green with



red and white bands. Antennal peduncles with thin, reddish, longitudinal stripe; flagella with 2-4 tan or green articles to every white article. Right chela white to light brown from merus to area of propodus at insertion of dactyl; dark brown L-shaped patch beginning at proximal end of propodus and ending at insertion of dactyl; adjacent mesial margins of dactyl and propodus darker brown. Left chela with similar coloring, L-shaped patch less defined. Second and third pereopods light brown, darker on dorsal and lateral surfaces. See Provenzano (1959) for additional coloration notes.

***Pagurus stimpsoni* (Milne Edwards and Bouvier, 1893)**

*Eupagurus stimpsoni*—Milne Edwards and Bouvier 1893:144, Plate 10, Figures 13-18.—Alcock 1905:182.

*Pagurus annulipes*—Schmitt 1935:206 (in part). [not *P. annulipes* (Stimpson)].

*Pagurus bonairensis*—Schmitt 1936:376.—Felder 1973:26 (in part), [not Plate 3, Figure 5].

*Pagurus hendersoni*—Wass 1963:144, Figure 5.

*Pagurus stimpsoni*—Lemaître et al. 1982:687, Figure 2.

**Material.** Station 14: 18 June 1992 (2o), 23 Jan. 1993 (1).—Station 18: 2 Oct. 1993 (3).—Station 30: 2 Oct. 1993 (1).—Station 32: 28 Oct. 1996 (1o).—Station 33: 29 Sept. 1996 (1o).

**Known range.** North Carolina to Florida; Gulf of Mexico; Caribbean coast of South America (Lemaître et al. 1982).

**Remarks.** Only 9 specimens of *P. stimpsoni* were collected at the mouth of Tampa Bay or in offshore waters. Specimens were found on hard substrates with *P. maclaughlinae* at Station 14, and *P. carolinensis* at Station 30. This species may have an unusually wide depth range. While most reports are from the shallow subtidal to depths of 30 m (Lemaître et al. 1982), Wass (1963) reported it in the Straits of Florida at depths of 228 m and 347-512 m.

Ovigerous females of *P. stimpsoni* were collected during the present study in June, September and October. Wass (1963) reported a gravid female from the Straits of Florida in August.

**Coloration.** Antennal flagellum with brown and white transverse bands. Pereopods with white and brown transverse bands. Chelipeds mottled brown and white; distal ends of dactyl and fixed finger white.

## DISCUSSION

### Distribution within the Tampa Bay Area

*Pagurus maclaughlinae*, *P. longicarpus* and *P. pollicaris* were distributed throughout the shallow waters of Tampa Bay and were often collected together. They were the only species taken in the upper part of the bay, including Old Tampa Bay and Hillsborough Bay (for subdivisions of Tampa Bay see Lewis and Whitman, Jr. 1985); however, no subtidal hard substrates were examined in these areas. Savercool and Lewis (1994) documented several hard-bottom communities in Old Tampa Bay and collections on these limestone outcroppings and oyster reefs may reveal additional hermit crab species. *Pagurus maclaughlinae* was found in a variety of subtidal habitats, but was the dominant species collected in seagrass beds. *Pagurus longicarpus* and *P. pollicaris* were most commonly taken in intertidal or shallow, subtidal waters on sand and sand/mud substrates. Because no seasonal quantitative sampling was conducted in subtidal areas, it was impossible to determine whether these 2 species underwent seasonal migrations. Along the Texas coast, both species are subtidal, but migrate to the upper subtidal zone briefly during the winter, presumably to breed (Fotheringham 1975).

*Clibanarius vittatus*, *Pagurus gymnodactylus* and *P. stimpsoni* inhabited shallow waters of the bay entrance near hard substrates, sand and seagrass beds. Four species, *Paguristes hummi*, *Paguristes* sp., *Petrochirus diogenes* and *Pagurus impressus* were collected from lower bay waters to offshore of Tampa Bay, mainly on hard substrate and sand habitats. *Paguristes puncticeps*, *P. sericeus* and *Pagurus carolinensis* were taken only offshore on hard substrates in depths of 5-15 m. Although several species were collected occasionally on high energy beaches, *Isocheles wurdemanni* appears to be the only species restricted to this habitat.

Hermit crab species richness was greatest on the hard substrate habitats of the bay entrance and shallow offshore waters where 12 of the 14 species found in the study were taken. The number of species decreased to only 3 in the lower salinity waters of upper Tampa Bay and less drastically in the deeper offshore waters.

### Zoogeography

Of the 15 species of hermit crabs reported previously from the shallow waters of the west coast of Florida (Table 1), 13 were found in the Tampa Bay area during this study. Only *Iridopagurus caribbensis* (Milne Edwards and Bouvier, 1893), *Paguristes tortugae* and *Pagurus brevidactylus* were not represented in the survey.

*Iridopagurus caribbensis* appears to be a rare species ranging from off South Carolina to the Caribbean Sea in depths of 10 to 180 m (Williams 1984). There is only one report of this species from the west coast of Florida (Table 1). *Paguristes tortugae* has been found from the Carolinas through the Caribbean to northern Brazil (Williams 1984). In the Gulf of Mexico, this species has been documented only along the coast of southwest Florida (Table 1). *Pagurus brevidactylus* ranges from Bermuda and northeast Florida through the Caribbean to northern South America (Lemaitre et al. 1982). Its only documented occurrence in the Gulf of Mexico is from northwest Florida, but the distribution of this species may extend to the Texas coast (McLaughlin 1975). It is highly probable that the species diversity of the hermit crab fauna of the Tampa Bay area is greater than the 14 species reported in this study. Only additional sampling, especially on the continental shelf, will help to determine the extent of the faunal richness of this area.

Tampa Bay is considered by some authors (Hedgpeth 1953, Rehder 1954, Earle 1969, Humm 1969) to be the boundary between the warm-temperate Carolinian province and the tropical Antillean province for marine organisms along the Gulf coast of Florida. The hermit crab fauna of the Tampa Bay area reflects the transition between these 2 provinces. Thirty-nine per cent of the species have widespread distributions including the U.S. east coast, Gulf of Mexico and Caribbean Sea (*Clibanarius vittatus*, *Petrochirus diogenes*, *Paguristes sericeus*, *Pagurus macLaughlinae*, *P. stimpsoni*). Five (39%) species have a temperate distribution and have been found along the U.S. east coast and the Gulf of Mexico (*Paguristes hummi*, *Pagurus carolinensis*, *P. impressus*, *P. longicarpus*, *P. pollicaris*). A lesser tropical influence is indicated by the presence of only 2 species (15%), *Isocheles wurdemanni* and *Paguristes puncticeps*, with distributions in the Caribbean and Gulf of Mexico only. One species, *Pagurus gymnodactylus*, appears to be endemic to the Gulf of Mexico. Although the Tampa Bay fauna contains elements from both provinces, as expected, there is no evidence to support the assertion that this area serves as a biotic boundary for shallow-water hermit crabs. McCoy and Bell (1985) came to the same conclusion about Tampa Bay.

### Symbionts

The porcellanid crab *Porcellana sayana* (Leach 1820) was associated with 4 hermit crab species collected in the Tampa Bay area. This species was found in shells with *Petrochirus diogenes* (Station 30), *Pagurus impressus* (Stations 30, 31), *Paguristes puncticeps* (Stations 26, 27) and *P. sericeus* (Stations 26, 27). While only one or 2 crabs

were typically found per hermit crab, 3 specimens of *Porcellana sayana* were collected with *Petrochirus diogenes*. *Porcellana sayana* appears to show little host specificity and has been reported with *Petrochirus diogenes* (Telford and Daxboek 1978, Williams 1984), *Pagurus pollicaris* (Williams 1984), *Paguristes grayi*, *Dardanus venosus*, the queen conch *Strombus gigas* (Telford and Daxboek 1978), and the decorator crab *Stenocionops furcata* (Hildebrand 1954). The large reported depth range of *Porcellana sayana*, shallow to 92 m (Gore 1974) and 713 m? (Schmitt 1935), has led to speculation that more than one species may be represented in these reports (personal communication D. L. Felder).

A male-female pair of bopyrid isopods tentatively identified as *Parathelges* sp. (personal communication R.W. Heard, Gulf Coast Research Laboratory, Ocean Springs, MS 39564) was found attached to the abdomen of a specimen of *Paguristes* sp. (Station 26).

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#### Appendix 1. Station data and occurrence of species.

- Southwest side of Courtney Campbell Causeway; sand/mud; 18.5-26‰ salinity; <1.5 m; triangular dredge. Species present: *Pagurus longicarpus*, *P. maclaughlinae*, *P. pollicaris*.
- Northwest side of Courtney Campbell Causeway; sand/mud; *Spartina* marsh; <1.5 m; dip net. Species present: *Pagurus longicarpus*.
- Southeast side of Courtney Campbell Causeway; sand/seagrass beds; <1.5 m; dip net; Species present: *Pagurus longicarpus*, *P. maclaughlinae*, *P. pollicaris*.
- Northwest side of Gandy Bridge; sand/mud, seagrass beds; 22‰ salinity; <1.5 m; dip net; Species present: *Pagurus longicarpus*, *P. pollicaris*.
- Picnic Island; sand/seagrass beds; 22-32 °C; 22-27‰ salinity; <1.5 m; dip net; Species present: *Pagurus longicarpus*, *P. maclaughlinae*, *P. pollicaris*.
- McKay Bay; mud/sand; dip net. Species present: *Pagurus longicarpus*.
- Hooker Point; dip net. Species present: *Pagurus pollicaris*.
- Spoil Island, Hillsborough Bay; dip net. Species present: *Pagurus pollicaris*.
- Ballast Point, sand/seagrass bed; 21-33.5 °C; 20-26‰ salinity; <1 m; dip net, hand collection. Species present: *Pagurus longicarpus*, *P. maclaughlinae*, *P. pollicaris*.
- Coffeepot Bayou; 1.5 m; hook and line. Species present: *Petrochirus diogenes*.
- Cockroach Bay; mud, oyster reefs, seagrass beds; 20-29 °C; 18-30‰ salinity; <1.5 m; dip net. Species present: *Pagurus maclaughlinae*.
- Piney Point; sand; <1.5 m. Species present: *Pagurus longicarpus*, *P. pollicaris*.
- Bishop Harbor, limestone outcroppings, sponges, sand; 27-32‰ salinity; 3.5 m; hand collection, SCUBA. Species present: *Paguristes hummi*, *Paguristes* sp., *Pagurus impressus*, *P. maclaughlinae*, *P. pollicaris*.
- Northeast Skyway Bridge jetty; sand, concrete blocks; 28-32‰ salinity; <3.5 m; hand collection, SCUBA. Species present: *Clibanarius vittatus*, *Petrochirus diogenes*, *Paguristes hummi*, *Paguristes* sp., *Pagurus gymnodactylus*, *P. impressus*, *P. longicarpus*, *P. maclaughlinae*, *P. pollicaris*, *P. stimpsoni*.
- Blackthorn Memorial Park; seagrass beds; 32‰ salinity; <1.5 m; dip net. Species present: *Pagurus impressus*, *P. maclaughlinae*, *P. pollicaris*.

16. Boca Ciega Bay. Species present: *Paguristes hummi*, *Pagurus impressus*.
17. Near Shell Key off Pass-a-Grille Beach. Species present: *Pagurus longicarpus*.
18. West Tierra Verde south of Pass-a-Grille Channel; sand, seagrass beds; 0.6 m; hand and tater rake/scoopert dipnet. Species present: *Paguristes hummi*, *Pagurus gymnodactylus*, *P. longicarpus*, *P. stimpsoni*.
19. Fort Desoto Beach; sand; <3 m; hand collection, snorkeling. Species present: *Pagurus impressus*, *P. longicarpus*, *P. pollicaris*.
20. Mullet Key Bayou; mud, seagrass beds; <1.5 m; dip net. Species present: *Clibanarius vittatus*, *Pagurus longicarpus*, *P. macLaughlinae*.
21. Mullet Key bayside. Species present: *Pagurus longicarpus*.
22. Fort Desoto Pier; sand, algal mats; <0.5 m; hand collection. Species present: *Pagurus longicarpus*.
23. Egmont Key, bayside; seagrass beds; 1.2 m; frame trawl with rollers. Species present: *Clibanarius vittatus*, *Petrochirus diogenes*.
24. 4 miles west of Egmont Key; sand, crushed shell; 6 m; dredge. Species present: *Paguristes hummi*.
25. 8 miles west of Egmont Key; sponge, coral, shell; 13.5-15 m; trawl. Species present: *Paguristes hummi*, *P. puncticeps*.
26. Larry's Ledge; sand, limestone outcroppings, corals, sponges; 32‰ salinity; 15 m; hand collection, SCUBA. Species present: *Petrochirus diogenes*, *Paguristes puncticeps*, *P. sericeus*, *Paguristes* sp., *Pagurus carolinensis*.
27. Jack's Hole; sand, limestone outcroppings, corals, sponges; 15 m; hand collection, SCUBA. Species present: *Petrochirus diogenes*, *Paguristes hummi*, *P. puncticeps*, *P. sericeus*, *Paguristes* sp., *Pagurus carolinensis*.
28. North Anna Maria Island front beach; sand; 3-4 m. Species present: *Isocheles wurdemanni*, *Paguristes hummi*, *Pagurus impressus*, *P. macLaughlinae*.
29. Molasses Barge off Anna Maria Island; sand, barge remains; 7 m; hand collection, SCUBA. Species present: *Paguristes* sp., *Pagurus impressus*.
30. St. Petersburg Artificial Reef; concrete, boat remains, sand; 10 m; hand collection, SCUBA. Species present: *Petrochirus diogenes*, *Paguristes hummi*, *P. puncticeps*, *Paguristes* sp., *Pagurus carolinensis*, *P. impressus*, *P. pollicaris*, *P. stimpsoni*.
31. 1 Mile Artificial Reef off Anna Maria Island; sand, 35‰ salinity; concrete pilings; 5-9 m; hand collection, SCUBA. Species present: *Paguristes hummi*, *Paguristes* sp., *Pagurus carolinensis*, *P. impressus*.
32. Egmont Key, front beach; sand; 35‰ salinity; 1.5 m; hand collection. Species present: *Pagurus gymnodactylus*, *P. stimpsoni*.
33. Egmont Key, front beach; concrete, fort remains; 24°C; 34‰ salinity; 3 m; hand collection, SCUBA. Species present: *Pagurus pollicaris*.
34. Lower Tampa Bay, off Lewis Island; shell; 3-4 m; otter trawl. Species present: *Pagurus macLaughlinae*, *P. pollicaris*.
35. Lower Tampa Bay, off Point Pinellas, seagrass beds; 2 m; otter trawl. Species present: *Pagurus macLaughlinae*, *P. pollicaris*.

# Gulf Research Reports

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Volume 11 | Issue 1

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The Planktonic Copepods of Coastal Saline Ponds of the Cayman Islands with Special Reference to the Occurrence of *Mesocyclops ogunnus* Onabamiro, an Apparently Introduced Afro-Asian Cyclopoid

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# THE PLANKTONIC COPEPODS OF COASTAL SALINE PONDS OF THE CAYMAN ISLANDS WITH SPECIAL REFERENCE TO THE OCCURRENCE OF *MESOCYCLOPS OGUNNUS* ONABAMIRO, AN APPARENTLY INTRODUCED AFRO-ASIAN CYCLOPOID

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**ABSTRACT** Taxonomic analysis of the copepod specimens collected from 29 Cayman Island ponds revealed the presence of ten species including the nearly ubiquitous cyclopoid *Apocyclops panamensis*. This species was widespread throughout the islands, being collected at 27 of the sampling sites. Another common calanoid, *Mastigodiptomus nesus*, occurred at nine sites on Grand Cayman and one on Cayman Brac. A cyclopoid of Afro-Asian origin, *Mesocyclops ogunnus*, was collected at two nearly fresh water sites on Grand Cayman and was considered to be a recent introduction. Because of its known adaptability to fluctuating environmental conditions, it is likely that *M. ogunnus* will successfully compete with and probably displace some of the native species and may become a dominant zooplankton on Grand Cayman.

## INTRODUCTION

The coastal saline ponds of the Cayman Islands represent a variety of habitats and, like those of most small Caribbean islands, are subject to hypersaline conditions during the dry seasons and flooding during the summer rainy season. Some ponds are also connected via sinks and seeps to brackish, anoxic, anchialine cave systems, and as such are somewhat affected by tidal flow. Coastal ponds provide a feeding habitat for a variety of resident and migratory waterfowl that forage on poeciliid fish and a variety of small benthic invertebrates including insect larvae, snails and crustaceans. In conjunction with a biological assessment conducted in 1996-97 by the Cayman Island National Trust, plankton samples were collected from 29 coastal and inland sites on Grand Cayman and the two sister isles, Little Cayman and Cayman Brac during August 1996 and January and June 1997. The habitats sampled included shallow roadside borrow pits and ponds, tidally influenced mangrove swamps, *Typha* swamps, sedge swamps, seasonal pools on grasslands, and the mouth of an anchialine cave. Salinities at most of the sampled locations varied from hypersaline in the fall and winter to nearly fresh in the summer when inundated during the extensive rainy period. A brief description of localities where copepods were collected is presented in Table 1 along with associated data on salinity (‰), temperature (°C), pH, and dissolved oxygen (D.O., mg/l). The general location of the collecting sites is shown on Figure 1.

## MATERIAL AND METHODS

Fifty non-quantitative plankton samples were taken using a plankton net with a mesh size of 0.07 mm at 29 coastal and inland pond localities in the Cayman Islands (Figure 1). All collections were taken from slightly below the surface of the water (0-0.5 m) by hand-towing the net a distance of about 10-15 m. Copepods were examined live soon after collection, and representative specimens were sorted from the sample, fixed with 10% formalin, and later preserved in 70% ethanol. Hydrographic data were collected within the upper 0.25 m at each site using a YSI multi-parameter system (model 85) and a pH pocket meter. Geographic coordinates were recorded with a portable GPS unit. Preserved specimens were examined by the senior author and identified to species with the aid of taxonomic descriptions published by Sewell (1940), Van de Velde (1984), Bowman (1986), Campos-Hernández and Suárez-Morales (1994), and Suárez-Morales et al. (1996).

## RESULTS AND DISCUSSION

Taxonomic analysis of the copepod specimens collected from Cayman Island ponds revealed the presence of 10 species. These included the nearly ubiquitous cyclopoid *Apocyclops panamensis* (Marsh 1913), which was widespread throughout the islands at 27 of the sampling sites, and the common calanoid, *Mastigodiptomus nesus* Bowman, 1986, which occurred at 9 sites on Grand Cayman and one on Cayman Brac. More isolated were the

TABLE 1

Cayman Island Pond station data and copepod occurrence records. GC = Grand Cayman, LC = Little Cayman, CB = Cayman Brac, NT = Not Taken. Key to species: AP = *Apocyclops panamensis*, AC = *Acartia tonsa*, MA = *Macrocyclus albidus*, MN = *Mastigodiatomus nesus*, ML = *Mesocyclops longisetus*, MO = *Mesocyclops ogunnus*, MJ = *Metis jousseaumei*, TT = *Thermocyclops tenuis*, TE = *Tropocyclops extensus*, TP = *Tropocyclops prasinus cf. aztequei*.

Site	Habitat	Date	Temp. °C	Salinity ‰	D.O. mg/l	pH	Copepod species
Betty Bay Pond, GC 19°17'50"N/81°11'30"W	Slightly brackish, borrow pit, mangrove/woodland fringe, <i>Chara</i> mats	1/16/97 6/11/97	29.8 34.4	2.6 5.8	5.9 4.0	9.5 9.6	MN, MO AP
Collier's Pond, GC 19°20'03"N/81°05'10"W	Permanent, shallow brackish, mangrove fringe, <i>Ruppia</i> beds	1/16/97 6/11/97	25.8 29.9	2.7 2.6	5.4 1.1	9.8 8.9	AP, MN AP
Governor's Pond, GC 19°16'39"N/81°18'30"W	Small inland <i>Typha/Urochloa mutica</i> fringe, seasonal, temporary	1/27/97 6/12/97	25.1 31.9	0.4 2.4	3.0 6.9	9.4 8.6	AP, MN, TP MN
Least Grebe Pond, GC 19°16'48"N/81°18'17"W	Small inland <i>Typha</i> /sedge fringe, seasonal, temporary	8/28/96 1/27/97 6/12/97	34.6 24.3 30.4	0.8 0.2 1.0	>13.0 1.53 1.05	8.9 9.4 8.4	MN, MO AP, MN, TP AP, MN
Malportas Pond, GC 19°20'35"N/81°12'17"W	Shallow, brackish, mangrove fringe	1/16/97 6/11/97	26.7 33.2	7.4 10.7	5.9 6.8	9.6 10.7	AP, MN AP
Meagre Bay, GC 19°17'38"N/81°13'44"W	Shallow, brackish, mangrove fringe	1/17/97 6/11/97	26.1 28.8	2.6 15.9	10.6 4.1	10.5 10.5	AP, MN AP
Palmetto Pond, GC 19°23'16"N/81°21'58"W	Shallow, brackish-hypersaline, mixed mangrove fringe	1/17/97 6/13/97	26.9 27.9	14.5 19.7	4.4 5.1	9.5 9.4	AP, MN AP
Pease Bay, GC 19°17'15"N/81°14'26"W	Shallow, brackish, mangrove fringe, rock outcroppings, <i>Ruppia</i> beds	1/16/97 6/12/97	30.0 30.0	1.6 19.5	10.5 1.9	10.1 10.1	AP, MN AP
Point Pond, GC 19°20'58"N/81°13'21"W	Shallow, brackish, temporary, mixed woodland fringe, <i>Ruppia</i> beds	1/26/97	32.0	5.8	12.7	11.2	AP, MN
Sea Pond, GC 19°23'14"N/81°22'32"W	Tidally influenced mangrove swamp	1/15/97	29.4	25.9	8.4	9.1	AT
Vulgunner's Pond, GC 19°23'10"N/81°22'59"W	Shallow, hypersaline lagoon, small tidal creek inlet, <i>Ruppia</i> beds	1/14/97 6/10/97	33.9 30.9	22.9 26.8	12.1 7.4	9.5 9.8	AP, TE AP, TT, MJ
Bittern Pond, LC 19°39'36"N/80°05'46"W	Marshland, Meagre fern ( <i>Acrostichum</i> ) fringe, <i>Ruppia</i> beds	6/3/97	28.9	2.1	6.5	9.1	AP
Booby Pond, LC 19°39'58"N/80°04'15"W	Seasonal, brackish-hypersaline, mixed woodland/mangrove fringe, rock outcroppings, sinkholes and underground seep influence	1/18/97 6/3/97	19.0 27.0	24.3 3.3	5.0 4.4	9.8 8.2	AP AP
Bulldozer Pond, LC 19°39'38"N/80°06'02"W	Marshland, seasonal, shallow, ironshore rock pools	1/20/97 6/4/97	23.0 29.0	21.9 5.0	4.0 3.8	9.3 9.9	AP AP
Coot Pond, LC 19°41'53"N/79°58'18"W	Temporary, seasonal, meadow pond, sedge fringe	6/5/97	31.0	0.1	0.1	7.9	ML, TT
Easterly Pond Complex, LC 19°41'56"N/75°59'14"W	Shallow, brackish, <i>Ruppia</i> beds	1/18/97	23.9	11.1	8.4	10.5	AP
Grape Tree Pond, LC 19°41'51"N/80°03'10"W	Shallow, brackish, mangrove/sea grape tree ( <i>Coccoloba</i> ) fringe	1/18/97 6/5/97	24.1 28.1	7.0 1.2	9.4 0.7	9.8 9.0	AP AP
Jackson's Pond, LC 19°41'26"N/80°03'54"W	Permanent, mangrove/mixed woodland fringe	1/19/97	22.1	10.8	13.0	9.9	AP

TABLE 1 (Continued)

Site	Habitat	Date	Temp. °C	Salinity ‰	D.O. mg/l	pH	Copepod species
Lighthouse Pond, LC 19°39'34"N/80°06'32"W	Seasonal hypersaline, connected to underground cave system	1/19/97 6/4/97	23.7 27.7	31.8 1.1	9.6 2.9	10.2 9.2	AP AP
McCoy's Pond, LC 19°40'26"N/80°05'49"W	Shallow, brackish, mangrove fringe	1/19/97 6/4/97	22.9 27.0	12.4 1.1	7.8 4.2	9.8 8.9	AP AP
Salt Rock Cave, LC	Mouth of anchialine cavesystem	6/6/97	NT	NT	NT	8.9	AP, MA
Sandy Point Pond, LC 19°42'05"N/79°53'53"W	Shallow, brackish, eutrophic	1/18/97 6/5/97	25.8 31.4	21.4 8.7	14.2 8.4	10.2 9.8	AP AP
Tarpon Lake, LC 19°40'41"N/80°02'27"W	Seasonal, brackish-hypersaline, old- growth mangrove swamp	1/18/97 6/3/97	23.4 25.9	8.5 5.2	4.2 4.9	9.8 8.3	AP AP
Westerly Pond -east site, CB 19°41'12"N/79°52'49"W	Narrow brackish inlet from main pond, mangrove fringe	1/21/97 6/8/97	23.0 27.8	11.1 2.8	11.2 1.3	10.5 8.7	AP AP
Westerly Pond -west site, CB 19°41'03"N/79°53'18"W	Shallow hypersaline, mangrove fringe	1/21/97 6/8/97	24.3 27.5	33.8 3.4	4.6 4.4	10.0 9.3	AP, MN AP, ML
Mangrove Wreck Pond, CB 19°41'14"N/79°52'10"W	Brackish, dredged canal adjacent to old growth mangrove swamp	1/21/97 6/7/97	23.4 28.4	16.3 2.8	7.1 6.2	10.3 9.2	AP AP
Red Shrimp Hole, CB 19°41'38"N/79°50'52"W	Marshland, ironshore rock pools, mangrove fringe, sinkhole connection to cave system	6/8/97	27.3	0.6	1.9	8.5	AP
Salt Pond, CB 19°41'16"N/79°51'49"W	Shallow, brackish-hypersaline, man-made levee on one edge	1/21/97 6/8/97	25.5 27.2	28.2 8.1	8.8 5.5	10.5 9.8	AP AP, TT
The Splits, CB 19°41'39"N/79°52'13"W	Interior brackish, karstic bluff formation	1/22/97	23.2	7.2	2.5	9.5	AP

occurrences of the predominantly freshwater cyclopoids, *Macrocylops albidus* (Jurine, 1820), *Mesocylops longisetus* (Thiébaud, 1914), *Thermocylops tenuis* (Marsh, 1909), *Tropocylops extensus* (Kiefer, 1931), *Tropocylops prasinus* cf. *aztequei* Lindberg, 1955, and *Mesocylops ogunnus* Onabamiro, 1957. Two species with greater tolerance for higher salinities, the harpacticoid *Metisjousseaumei* (Richard, 1892) and the calanoid *Acartia tonsa* Dana, 1852, were limited to single occurrences at Vulgunner's Pond and Sea Pond, sites on Grand Cayman with direct marine influence.

Most of these species have been previously recorded from Grand Cayman (Reid 1990), and the overall biogeographic affinities of the local copepod community are clearly tropical. The most noteworthy record is that of *Mesocylops ogunnus*, an apparently introduced Afro-Asian species, found at Least Grebe, Grand Cayman, and Betty Bay Pond, Grand Cayman, 2 nearly freshwater sites. It can be distinguished from the known American species of *Mesocylops* by the presence of a row of spines on the maxillular palp, a character shared only with the African *M. salinus* Onabamiro, 1957. Other diagnostic characters of *M. ogunnus* include: pediger 5 with several lateral and a

few dorsal spines, seminal receptacle with broad lateral arms and a long curved pore-canal, caudal ramus with naked medial surface and with spines at the bases of the lateral and lateral most terminal caudal setae (Van de Velde 1984, Reid and Pinto-Coelho 1994).

*Mesocylops ogunnus* is distributed in Nigeria, Subsaharan Africa, the Near East, South and Southeast Asia, and Brazil. This species inhabits a wide variety of freshwater environments, and is one of the most eurytopic species of *Mesocylops* in the Afro-Asian region (Van de Velde 1984, Jeje and Fernando 1992, Reid and Pinto-Coelho 1994). This adaptive capacity would explain the success of this species when introduced into a new environment. In the Cayman Island system, *M. ogunnus* is not widely distributed, nor present in a variety of environments. This suggests that the invasion of *M. ogunnus* in the Cayman Islands is quite recent, since, like many other introduced copepods, *M. ogunnus* is a very efficient competitor and can exploit different types of environments (Reid and Pinto-Coelho 1994). Were this species long established in the Caymans, we would expect it to be common and abundant. A more thorough investigation into similar sites throughout the year would

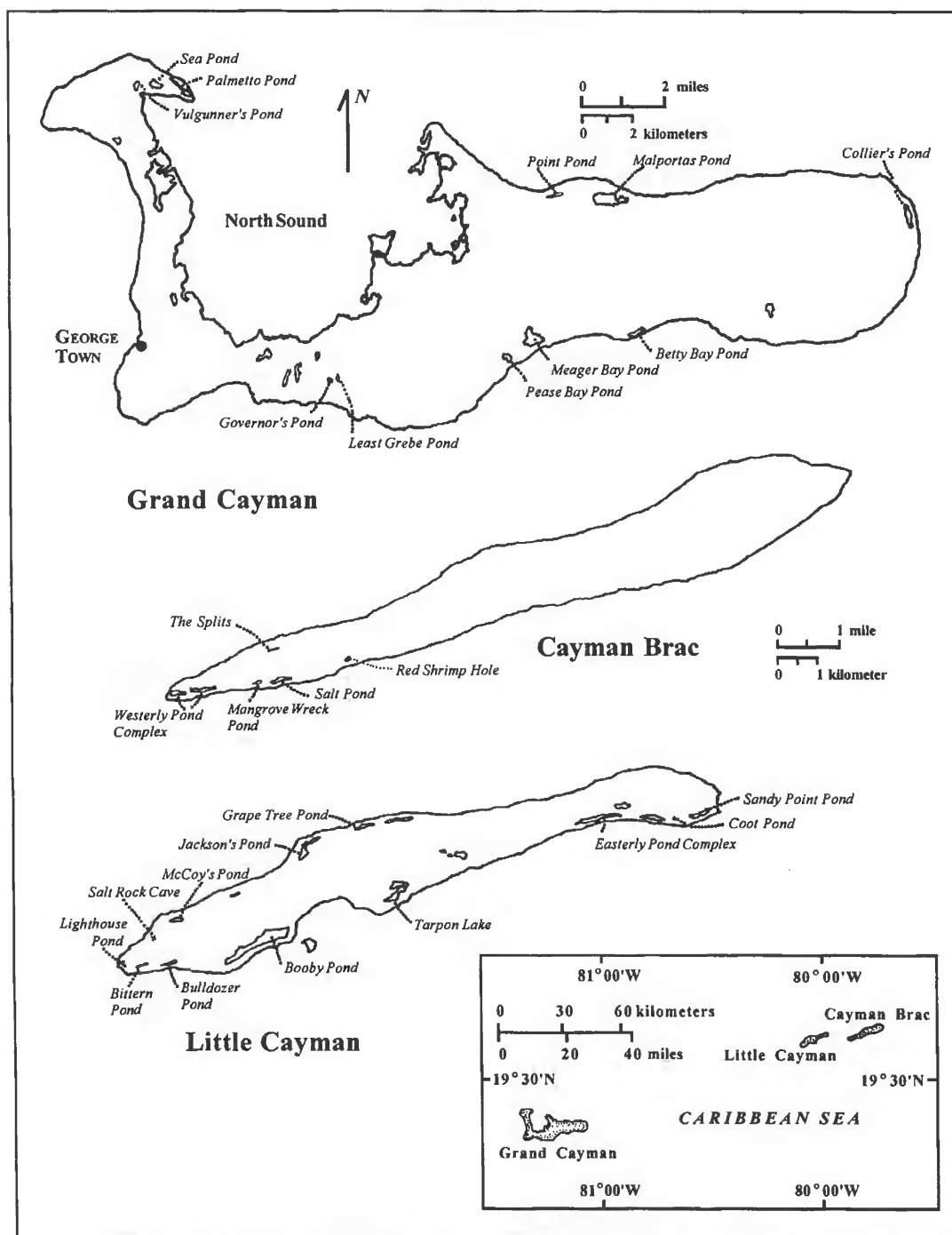


Figure 1. Cayman Islands, British West Indies showing the location of coastal saline ponds where copepods were collected. Inset shows relative location in the Caribbean Sea and distances between the 3 islands.



likely better define the extent of the *M. ogunnus* invasion into the Cayman Islands. The adaptability of *M. ogunnus* to differing environmental conditions leads us to anticipate that it will successfully compete with and probably displace some of the native species and may become a dominant zooplankton in the area.

It is probable that *M. ogunnus* has been transported along with aquaculture organisms to other parts of the world, since it has been recorded from aquaculture ponds in the Ivory Coast. Aquacultural activities have apparently effected the introduction of several species of copepods. For example, the Asiatic calanoid, *Boeckella triarticulata*, was apparently introduced to Italy together with Chinese carp. *Pseudodiaptomus marinus*, another Asiatic calanoid, was possibly introduced in a similar manner into the United States. *Pseudodiaptomus trihamatus* of the Indo-Pacific may have been introduced to Brazil with the shrimp *Penaeus monodon*. Finally, *Mesocyclops ruttneri*, an East-Asian cyclopoid was perhaps introduced to the Southern U.S. by rice culture (reviewed by Reid and Pinto-Coelho 1994).

The other copepods found in the Cayman Island ponds we sampled (species of *Tropocyclops* and *Apocyclops panamensis*) have different ecological niches and may not be competitors of *M. ogunnus*. *Apocyclops panamensis*, the most abundant species in the Cayman Island ponds sampled, was introduced to the Ivory Coast from Western Atlantic coasts (Dumont and Maas 1988). The only calanoid found in the Cayman Island ponds is *Mastigodiptomus nesus*; however, the specimens recorded during this survey lack the characteristic dorsal keel described by Bowman (1986) for this species.

*Thermocyclops tenuis* had previously been recorded only from Grand Cayman (Reid 1990), and the new records from Little Cayman and Cayman Brac represent a modest range extension for this cyclopoid. Specimens from this area have been deposited at the National Museum of Natural History, Smithsonian Institution (USNM-268059).

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Variations in the Ventral Ciliature of the Crustacean Symbiont Hyalophysa (Ciliophora, Apostomatida) from Mobile Bay and Dauphin Island, Alabama

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# VARIATIONS IN THE VENTRAL CILIATURE OF THE CRUSTACEAN SYMBIONT *HYALOPHYSA* (CILIOPHORA, APOSTOMATIDA) FROM MOBILE BAY AND DAUPHIN ISLAND, ALABAMA

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**ABSTRACT** Apostome ciliates are symbiotic organisms whose life cycles are complex and involve specific feeding, divisional, migratory, and phoretic stages. In this study we examined apostome trophonts (the diagnostic stage) from a variety of crustacean hosts in the Mobile Bay and Dauphin Island, Alabama, area. The hosts were grass shrimp (*Palaemonetes pugio* and *P. paludosus*), striped hermit crab (*Clibanarius vittatus*), blue crab (*Callinectes sapidus*), and pink shrimp (*Farfantepenaeus* (= *Penaeus*) *duorarum*). A number of similar but distinct morphotypes of apostomes were present, those corresponding to descriptions of species of *Hyalophysa* as well as variant forms. The morphotypes observed in this study had the following characteristics: variations in the formation of the anterior ventral field of kinetosomes from falciform field 9; variations in the degree to which ciliary row 1 (kinety 1) was separated into 2 segments; and variations in the development of kinety a. A record of the variant morphotypes that do not correspond exactly to an established species should prove useful to biologists attempting to identify apostomes from crustacean molts. We choose not to name the variant forms as new species because they exist as different morphotypes within a population of cells, because some of these types occur in low frequency, and because one of the variant forms changes from one morphotype to another.

## INTRODUCTION

Bradbury (1966) established the genus *Hyalophysa* in 1966 for the organism *H. chattoni*, a common apostomatous ciliate associated with crustaceans in North America. This symbiont spends most of its life cycle encysted on a host such as a shrimp or crab, waiting for a chemical signal to indicate that the host will soon molt. After receiving the signal, the ciliate metamorphoses from a quiescent phoretic cell to a trophont (macrostome) that will excyst upon ecdysis of the crustacean (Figure 1). The trophont then swims to the inside of the exoskeleton and feeds by pinocytosis on the exuvium contained within. Following this single opportunity to feed, the ciliate settles on a substrate, encysts, and produces daughter tomites. The tomites (microstomes) are migratory cells with a non-functional mouth that settle on a crab or shrimp to encyst and begin the cycle again.

Exuviotrophic apostome ciliates are ubiquitous organisms, reported from a wide variety of crustaceans in North America including members of the genera *Pagurus*, *Clibanarius*, *Palaemonetes*, *Cambarus*, *Uca*, *Upogebia*, *Callinectes*, *Sesarma*, *Penaeus*, *Alpheus*, *Lophopanopeus*, *Cancer*, *Panopeus*, and *Carcinides* (Bradbury 1966, Bradbury and Clamp 1973, Grimes 1976, Johnson 1978). Only one report exists in the recent literature that surveys apostomes from a number of hosts from the same locale (Grimes 1976). The present study was undertaken to better understand the apostomes of the Dauphin Island and Mobile Bay region in Alabama by sampling the apostome trophonts feeding in the molts of

a variety of crustaceans. The hosts examined in this study were *Palaemonetes pugio*, *P. paludosus*, *Clibanarius vittatus*, *Callinectes sapidus*, and *Farfantepenaeus* (= *Penaeus*) *duorarum*. Penaeid shrimp names are based on Pérez Farfante and Kensley (1997).

We report many different apostome morphotypes including *H. chattoni* (Bradbury 1966), a number of variants similar to *H. chattoni*, as well as variant forms that do not exactly match published species descriptions. These morphotypes illustrate the variation that occurs in the ciliature within apostome species from one host to another, and provide insights to the transformation from the phoront to the trophont.

## MATERIALS AND METHODS

Grass shrimp (*P. pugio*), blue crabs (*C. sapidus*), and striped hermit crabs (*C. vittatus*) were collected with a dip net or by hand in the airport road marsh, Dauphin Island, Alabama (30°15'N, 88°07'W). Pink shrimp (*F. duorarum*) were collected by throw net from the eastern end of Dauphin Island (30°15.03'N, 88°04.60'W), and the grass shrimp *P. paludosus* was collected by dip net at Meaher State Park in Baldwin County, Alabama (30°39'N, 87°55'W) between the mouths of the Apalachee and Blakeley rivers. The animals were kept at the main campus of Troy State University in filtered water obtained at the collection site and were fed flaked or pelleted fish food every other day. Their water was changed approximately once a week,

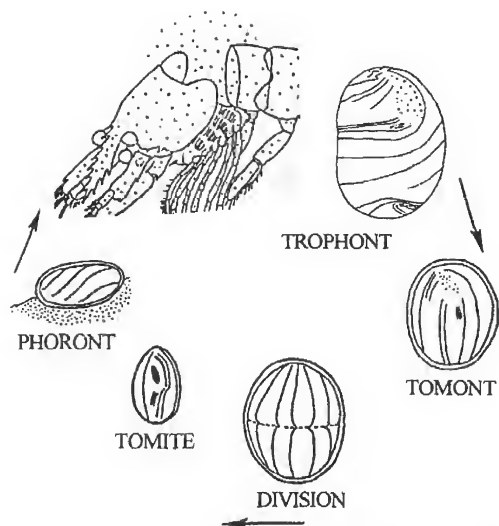


Figure 1. The life cycle of the apostomatous ciliate *Hyalophysa*. Clockwise from the top: trophonts within the exoskeleton, tomonts undergoing division while encysted on the substrate, the swimming infestive tomite, the encysted phoront. Line drawings of the cells are based on silver nitrate impregnation. Adapted from Landers et al. 1996.

Grass shrimp were housed in large groups and only isolated in glass bowls prior to molting. The premolt shrimp were identified by the presence of the developing setae visible under the old exoskeleton in the uropods (Freeman and Bartell 1975). Crabs and prawns were kept in isolation at all times due to the difficulty in identifying premolt organisms. Following ecdysis, the apostomes swimming in the exoskeleton were pipetted directly out of the molt for fixation and silver impregnation.

The ciliates were fixed in 2.5-5% glutaraldehyde for 5-15 minutes. After a thorough washing in distilled water, the cells

were enrobed in warmed gelatin and impregnated with silver nitrate following a modification of the Chatton-Lwoff method (Bradbury and Clamp 1973). Following silver impregnation the cover slips were immersed in cold 70% ethanol, dehydrated, cleared in xylene, and mounted with resin.

## RESULTS

A variety of different apostome morphotypes were observed (Figures 2-10) which had the following 3 characteristics: variations in the dissolution of falciform field 9 (FF9) to form an anterior ventral field of kinetosomes (AVF); variations in the degree to which ciliary row 1 (kinety 1 or K1) was separated into 2 segments; and variations in the development of kinety  $\alpha$  (K $\alpha$ ) from FF9. During this study we did not observe variations in the dorsal or the posterior ventral ciliature of the trophont stage, but only differences involving the above named characteristics. Though a gradation of morphotypes exists, the cells that are most representative of the data are illustrated in Figures 2-10. The numbers of each cell type are referenced by the host crustacean in Table 1.

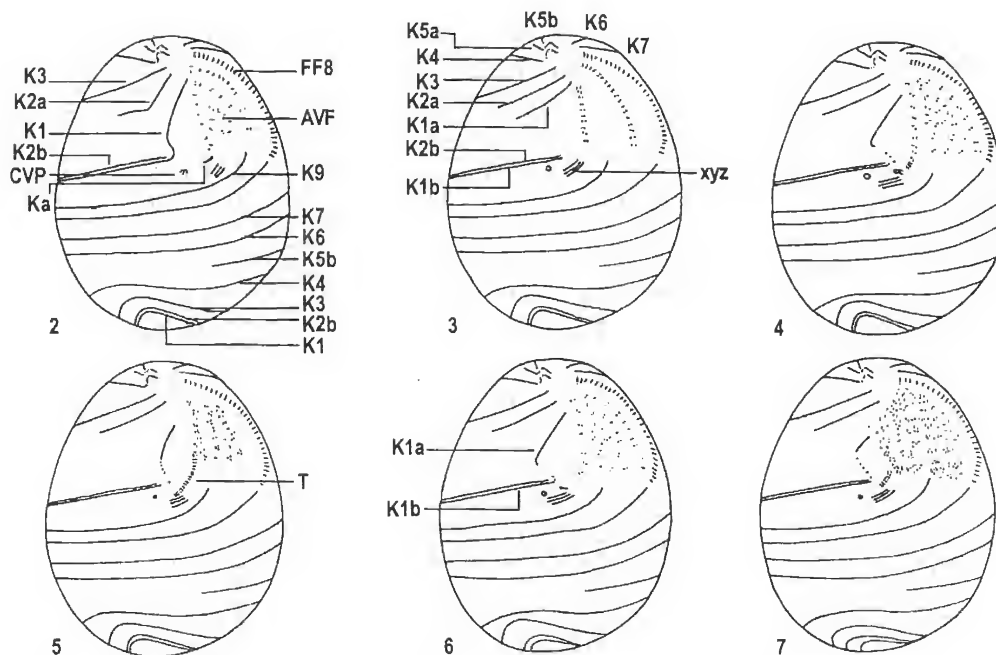
### Apostomes from *Clibanarius vittatus*

Few trophonts (5) were identified from the striped hermit crab, though all exhibited the type ciliature originally described for *H. chattoni* (Figures 2 and 8). This ciliature has been described previously (Bradbury 1966). A brief description of the cell follows: The cell is oval to reniform and measures approximately 55 x 30  $\mu$ m (the size is variable depending upon the amount of ingested food). Nine kineties spiral dextrally around the cell from the anterior to the posterior end. Kinety 1 extends posteriorly along the anterior third of the cell, then bends sharply to the right and continues around the cell. Kinety 2 is divided,

TABLE 1

Listing of all apostome ciliates and their hosts (#observed/#examined). The ciliates are referenced by Figure number from this article and by host. \*Data from morphotype #4 and #5 combined.

Host	Figure #					
	2	3	4	5	6	7
<i>Clibanarius vittatus</i>	5/5					
<i>Callinectes sapidus</i>	1/15		11/15		3/15	
<i>Farfantepenaeus</i> (= <i>Penaeus</i> ) <i>duorarum</i>	1/27	7/27	17/27		2/27	
<i>Palaemonetes pugio</i>	18/95	3/95	65/95*	65/95*	1/95	8/95
<i>Palaemonetes paludosus</i>			5/17		12/17	



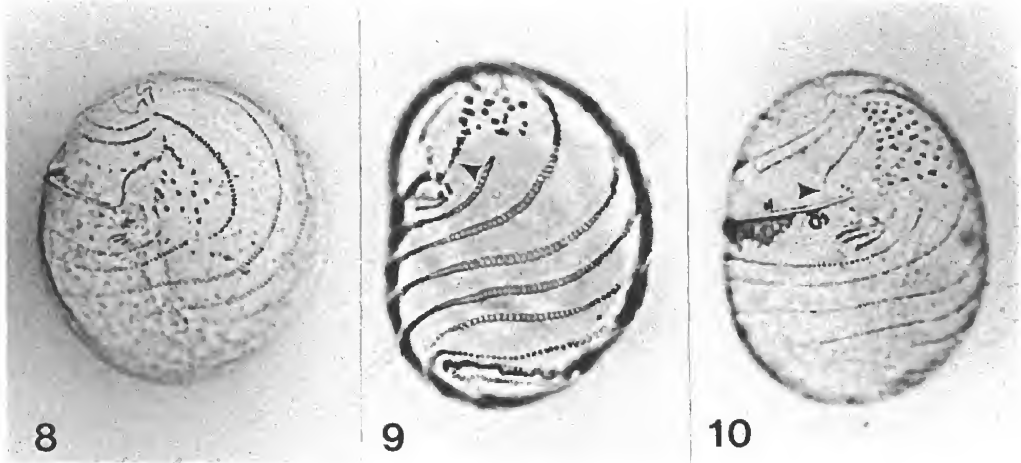
Figures 2-7. The ventral ciliature of trophonts of *Hyalophysa*. Line drawings based on silver nitrate impregnation. Solid lines indicate ciliary rows (kineties). Individual dots represent kinetosomes. K = kinety, CVP = contractile vacuole pore, FF = falciform field, AVF = anterior ventral field, Ka = kinety *a*, xyz = kineties *x*, *y*, and *z*, T = kinetosomal tail. Figure 2. *Hyalophysa chattoni* type morphology. Figure 3. *H. chattoni* variant with a poorly developed AVF. FF9 has divided into two rows but has not broken into an AVF. Figure 4. *H. chattoni* variant with an altered K1 and AVF. Note the kinetosomal tail, derived from FF9, at the lower right corner of the AVF. Figure 5. *H. chattoni* variant with an altered K1 and AVF. Note the kinetosomal tail, derived from FF9, at the lower right corner of the AVF. Figure 6. *H. chattoni* variant. Note the separation of K1 to form a K1a and K1b and the absence of a kinetosomal tail on the AVF. Figure 7. *H. chattoni* variant. Note the large AVF, kinetosomal tail, and altered K1.

forming a K2a and K2b. Kinety 2a runs along the left of K3. Kinety 4 has a crook at the anterior end and extends around the cell to the posterior. Kinety 5 is divided into K5a, a short Z-shaped fragment, and K5b, which bends around the cell and terminates on the mid-ventral surface. Kinety 6 and K7 spiral from the anterior pole to the posterior pole. The posterior portion of K8 is similar to K6 and K7, but anteriorly it is a double row of kinetosomes termed the Falciform Field (FF8). Kinety 9 parallels K8 on the right. Anteriorly K9 is broken into a field of scattered kinetosomes termed the Anterior Ventral Field (AVF). Three short kineties (*x*, *y*, and *z*) are located to the left of the contractile vacuole pore between K9 and K1. Kinety *a* is a short kinety located anterior to *xyz*.

**Apostomes from *Farfantepenaeus* (= *Penaeus*) *duorarum***  
*Hyalophysa* spp. trophonts from *F. duorarum* molts were variable in many respects. In 7 of 27 cells the FF9 did not

break apart to form an AVF but instead formed one to 3 doubled rows of kinetosomes that occupied the area between FF8 and K1a (Figure 3). Additionally, K1 was divided into a K1a and K1b, with K1a completely separated from its lower segment and aligned along the left side of K2a. Kinety *a* was not observed in these trophonts. This morphology is an intermediate form between *Hyalophysa* and *Gymnodinioides* (Bradbury 1966, Chatton and Lwoff 1935).

The majority (17 of 27) of the trophonts from *F. duorarum* were similar to the *H. chattoni* variant illustrated in Figure 4. In this type, FF9 divided into scattered groups of 2 to 4 kinetosomes to form an AVF and possessed a tail of doubled kinetosomes in the lower right corner, derived from the remnant of FF9. Kinety *a* was observed in this type. Kinety 1 was either divided into a separate K1a and K1b, separated by a few scattered kinetosomes, or K1a was connected to K1b but appeared to be stretched away from its lower fragment. In addition to this cell type, 2 of



Figures 8-10. Photomicrographs of selected silver-stained apostomes. Figure 8. *Hyalophysa chattoni* type specimen from *Palaemonetes pugio*. The cell is approximately 81  $\mu\text{m}$  wide. Figure 9. *H. chattoni* variant from *P. pugio*. Note the kinetosomal tail (arrowhead). The cell is approximately 59  $\mu\text{m}$  wide. Figure 10. *H. chattoni* variant from *Callinectes sapidus*. Note the break in K1 (arrowhead). The cell is approximately 75  $\mu\text{m}$  wide.

27 cells possessed no tail (Figure 6) and one cell was a type specimen (Figure 2).

#### Apostomes from *Callinectes sapidus*

Most of the trophonts (11 of 15) observed from the blue crab had a morphology similar to the trophont that was most common on *F. duorarum* (Figure 4). K1 was either stretched to the point of separation or was divided into a K1a and K1b and separated by a short gap occupied by 3 to 4 kinetosomes. An AVF was fully formed, with a tail of kinetosomes present in the lower right corner that varied from short (4 kinetosomes) to much more defined (8 kinetosomes). Kinetotaxia was present in these cells, either attached to the tail of kinetosomes or separate from it. In addition to this cell type, 3 cells from *C. sapidus* had no tail (Figure 6) and one was similar to the type morphology of *H. chattoni* (Figure 2).

#### Apostomes from *Palaemonetes pugio*

A large number of cells from *P. pugio* were examined with the majority of the cells (65 of 95) similar to the morphologies illustrated in figures 4 and 5. In these cells a tail of kinetosomes is found at the posterior right corner of the AVF, varying in size from 6 kinetosomes (Figure 4) to 36 (Figure 5). The average number of kinetosomes in the tail was 14 ( $N = 33$ ). K<sub>2</sub>a had usually not yet separated from the kinetosomal tail of the AVF. The 30 remaining cells represented a variety of morphologies. Eighteen of the cells were the type morphology (Figure 2), 3 cells had a FF9 that was divided into 2 or 3 fragments rather than an

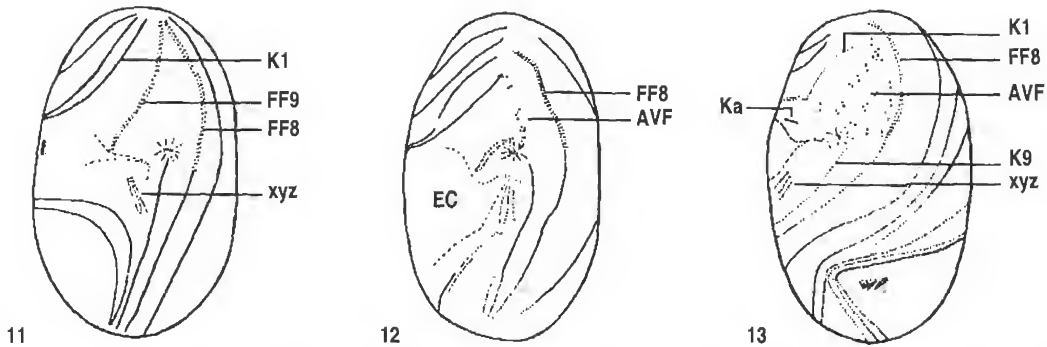
AVF (Figure 3), and one cell had a type AVF but a broken K1 (Figure 6). Finally, 8 cells possessed a large AVF in which individual kinetosomes were spread out into a large shield-shaped field (Figure 7). A tail of kinetosomes was present and K1a was shortened, connected to K1b by scattered kinetosomes. The AVF of this apostome is similar to that of *H. trageri* (Grimes 1976).

#### Apostomes from *Palaemonetes paludosus*

Trophonts from the molts of *P. paludosus* were similar to one of 2 morphologies. Five of 17 cells had a short kinetosomal tail and a bend or break in K1, as seen in apostomes from *C. sapidus*, *P. pugio*, or *F. duorarum* (Figure 4). The remaining cells (12 of 17) had no kinetosomal tail and a separated or bent K1 (Figure 6). Of the last group of cells, 2 had a K1a that did not curve towards K1b but instead was aligned close to K2a. Those 2 cells were most similar to the freshwater apostome *H. bradburyae* (Landers et al. 1996).

#### DISCUSSION

In this study we have demonstrated a number of apostome variants. Particular variants are not restricted to specific species of hosts, but rather, are found in mixed populations on a number of crustaceans. All of the variations result from subtle differences that occur in the cell during the transformation of the phoront stage to the trophont (Figures 11-13). Of all of the changes that take place during this transformation, the formation of the AVF



Figures 11-13. Line drawings illustrating the metamorphosis of the phoront to the trophont during the premolt period on the host (adapted from Landers 1986). Note the formation of the AVF from FF9. K = kinety, FF = falciform field, AVF = anterior ventral field, Ka = kinety a, xyz = kineties x, y, and z, EC = developing extended cystostome.

from FF9 and the bend in K1 are the most variable. The 4 nominal species of *Hyalophysa* are differentiated by characteristics of the AVF and K1, among other features (Bradbury 1966, Bradbury and Clamp 1973, Grimes 1976, Landers et al. 1996). We report variations in the trophont ciliature that involve 3 key characteristics, the AVF, Ka, and K1.

The dissolution of FF9 is a process that occurs normally during the phoretic stage of *Hyalophysa* to form the AVF (Bradbury and Trager 1967). Landers (1986) described this metamorphosis using protargol silver impregnation (see Figures 11-13) and suggested that Ka is a derivative from the posterior fragment of FF9. This hypothesis is confirmed by the present data. Variant forms in which a tail of kinetosomes exists clearly show Ka connected to the posterior tip of the AVF tail.

Kinety 1 is a variable structure among the *Hyalophysa* species. In the *H. chattoni* type morphology, not often seen in this study, K1 has a sharp 90° bend to the right as it extends posteriorly along the right border of the cystostome. This bend is also found in *H. trageri*. In *H. lwoffii* and *H. bradburyae* K1 is divided, though the position of the anterior segment differs. In the present study K1 was most often stretched into either 2 kineties that were barely connected or they were separated by a gap occupied by scattered kinetosomes. Conversely, a wide separation was observed between K1a and K1b in some apostomes from *P. paludosus*, a characteristic more similar to the freshwater form *H. bradburyae* than to *H. chattoni*. A wide separation between K1a and K1b was also present on apostomes with an undeveloped AVF (Figure 3).

The morphotypes described in this report were chosen as representatives to reflect the many variations we observed. One morphotype matches that of a described species (Figure 2) whereas other forms have characteristics

that do not correspond to established species. For example, the cell illustrated in Figure 3 is intermediate between *Gymnodinioides* and *Hyalophysa*. We think this form should currently be considered a variant of *H. chattoni*, and not a species of *Gymnodinioides* because the later genus possesses an unbroken K1, and FF9, if present, is unbroken (Chatton and Lwoff 1935, Bradbury et al. 1996). The cells illustrated in Figures 4 and 5 are similar to *H. chattoni* though in these forms the posterior tip of FF9 has not completed its transformation and remains as a tail of kinetosomes on the ventral surface. The cell in Figure 6 is similar to *H. chattoni* if K1a points posteriorly towards K1b, as illustrated. However, if K1a is more closely aligned next to K2a, the cell is similar to *H. bradburyae*, a freshwater form (note: this form on *P. paludosus* is not surprising, because the shrimp were caught near the Apalachee and Blakeley rivers where a freshwater apostome might be expected). The cell in Figure 7 is similar to the *H. chattoni* variants in Figures 4 and 5 as well as to *H. trageri* (a species known only from the genera *Sesarma* and *Uca*). It is similar to *H. trageri* because of the large shield shaped AVF, but differs from that species in having a kinetosomal tail on the AVF and having a separated K1. At this time we are reluctant to assign the variants illustrated in Figures 2-7 to new taxa because they exist as different morphological types within the same population of cells and because of the low frequency of some of the variant types. Additionally, we have observed that the cells illustrated in Figures 4 and 5 transform into the *H. chattoni* type morphology after feeding has ended (Zimlich, manuscript in preparation), suggesting that some of the variants represent a lag in the development of the *H. chattoni* trophont.

It should be pointed out that some of these variant types are not restricted to Alabama, though they, and not



the established taxa, represent the dominant types from the Mobile Bay area. Neptun (1988) reported the variant illustrated in Figure 5 from *P. pugio* in North Carolina, though it was rarely seen there. Also, the variant described in Figure 3 from *F. duorarum* was found (rarely) in molts of *P. pugio* in North Carolina (S. Neptun, personal communication).

Although different species of apostome trophonts are morphologically distinct, other stages in the life cycle such as the tomont and tomita are remarkably similar to one another (Chatton and Lwoff 1935). In the trophont the cilia are apparently not involved in feeding and can vary in position without affecting the cell. Our data support this hypothesis, since cells of all morphologies bloated normally as they fed within the host's exoskeleton.

Many hypotheses and future experiments can be designed to address the question of why these variants exist and whether the variation in the ventral ciliature has a functional or developmental significance. As the ventral ciliature does not appear to affect the feeding process it is possible that this variation has evolved within the species because there are few selective pressures to restrict the patterning of this ciliature. All of the species of *Hyalophysa* revert to a common morphology as they encyst and produce daughter tomites, suggesting that developmental restraints exist during tomitogenesis that do not allow for as much morphological variation in later stages. There are many factors that could play a role in determining the subtle morphological differences of the trophont's ventral ciliature, such as diet, host animal, water temperature, season, and pollution effects. It is also possible that the morphotypes exist as a result of genetic variations within the population that are not immediately influenced by environmental factors. Future avenues of research are plentiful in this area. For example, apostomes from one host could be used to infect other crustaceans to see if the proportion of the variant types changes with the host. Also, a clonal population of cells could be produced from one trophont and carried through many molt cycles on cleaned shrimp to see if morphological variations are present. Many other experimental variables could be tested in the laboratory to further analyze possible causes of variations in the trophont.

In their historic monograph, Chatton and Lwoff (1935) separated the apostomes into a number of distinct groups based on their diet and life cycles. This study has focused on only one group, the exuviotrophs, whose diet consists of exuvial fluid from crustacean exoskeletons. Earlier reports (Chatton and Lwoff 1935, Bradbury 1966, Grimes 1976, Lindley 1978) leave little doubt that exuviotrophic apostomes exist on probably all crustaceans ranging from

decapods to amphipods to barnacles. While previous reports acknowledge exuviotrophic apostomes, probably of the genus *Hyalophysa*, from the shrimp, *Farfantepenaeus aztecus*, *F. duorarum*, *F. brasiliensis*, *Litopenaeus (=Penaeus) setiferus*, and *L. vannamei*, (Johnson 1978, Lotz and Overstreet 1990), our study confirms the presence of *Hyalophysa chattoni* variants on the pink shrimp, *F. duorarum*, and extends the known record of the genus *Hyalophysa* to a variety of crustacea from the Mobile Bay region. This record establishes the variability present in the apostome population of this region.

Additionally, we have observed apostome trophonts within molts of the mole crab *Emerita* spp. from Dauphin Island but were not able to obtain satisfactory silver stains. Future studies of apostomes will attempt to determine the exuviotroph fauna of crustacea from the high energy beach zones.

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# GORDON PENNINGTON GUNTER

## 1909-1998

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... if you are interested in marine science or any other science, you run along as fast as you can go. Other things are just an interference, they just take up your time. (Gordon Pennington Gunter)

Gordon Pennington Gunter was born in the Red River country of north Louisiana, Natchitoches Parish, in the town of Goldonna, on August 18, 1909, or "about 44 years after the death throes of the Confederacy", as Gunter described his birth year. Gunter also recorded that his father, John Osbon Gunter, had been born in Creston, Louisiana, in 1876, or "about the year the last of the Yankee soldiers left." Gordon Gunter's grandfather, Miles Osbon Gunter, served as a cavalryman under Fighting Joe Wheeler. Gunter recalled his mother saying his great-grandmother died during the War because, "She was old and tired and sick and did not have enough to eat." Dr. Gunter attributed her death to the result of Sherman's March to the Sea. Gunter remained somewhat cool toward the memory of William Tecumseh Sherman and usually spoke pejoratively about the General. Gunter described seeing an old Confederate Veteran hurrying along on New Orleans' Royal Street in 1931. The old veteran was dressed in the old butternut uniform of the Confederacy, and Gunter hurried along to overtake him, just to touch him. Gunter could not overtake the old man in the crowd and that was the last Confederate soldier he was ever to see. It was inevitable that with these sensitivities Dr. Gunter should find himself involved with The Sons of Confederate Veterans and The Order of the Stars and Bars, organizations devoted to the preservation of respect and honor for those men who had served as Confederate Soldiers. Dr. Gunter served that organization long and faithfully and rose to become Commandant of the organization at the state level. In keeping with his ecumenical view, it should be pointed out that Dr. Gunter was also a member of The Sons of the American Revolution.

Gordon Gunter had gone off to Louisiana State Normal College with the idea that he might become an attorney, like his father, or perhaps become a French scholar. He abandoned both those ambitions immediately after being

exposed to his first biology course, which interestingly enough was mandatory, rather than elective. That course seemed to have been a turning point in Gunter's life as he proceeded to earn a B.A. in zoology, securing that degree in 1929. With that degree in hand he went to the University of Texas with the intention of becoming a bacteriologist and earned the M.A. degree in 1931. Upon completion of the master's degree, Gunter worked on shrimp and oysters in Louisiana, Florida and Texas, and on fishes in California, during the Debris Dam Fisheries Survey for the U. S. Engineers Office. Dr. Gunter was always nattily dressed and he did not go about during business hours without a jacket and necktie. Years earlier Gunter had been admonished by his mentor, Professor Williamson of Louisiana State Normal College, for going about the campus

improperly dressed, that is to say *sans* necktie. He seemed never to have forgotten the instruction in dress and at some level it might have embarrassed him. It could be pointed out that the omission of the necktie could have been due to youthful exuberance and just sheer excitement associated with being at school, because Gunter also recalled that his father had bought him a fine red gelding to go back and forth to school on, and in the excitement at his first day of matriculation, young Gunter clanked about in the college halls throughout most of the first day, oblivious to the fact that he was still wearing his roweled riding spurs.

In 1932 Gunter married his first wife, Carlotta "Lottie" Gertrude La Cour. They produced a daughter, Charlotte Anne Gunter Wood Evans of Galveston, Texas, and two sons, Miles Gordon Gunter and Forrest Patrick Gunter of Austin, Texas. Dr. Gunter took measureless pride in these children. For many years the single bit of decoration in Gunter's office was a big photograph of his son, Gordon, in his Marine dress whites. The younger Gordon Gunter barely survived injuries sustained in a fiery helicopter



crash in the Philippines, en route to Marine duties in Vietnam. He is today a successful attorney in Austin, Texas.

Gunter had returned to the University of Texas in 1939 as an instructor in physiology and had a concurrent appointment as a marine biologist to the Texas Game, Fish and Oyster Commission. During this time he was lured into the study of physiology and zoology by Professor Elmer Julius Lund, and Gunter completed his doctoral work in those disciplines in 1945. After a great deal of work by Dr. Lund, the University of Texas founded the Institute of Marine Science at Port Aransas in 1945. Gunter, after receiving his Ph.D., conducted research there, becoming acting director of the Institute from 1949 to 1954, then director until he left in 1955 to come to Mississippi. Lund had also established *Publications of the Institute of Marine Science* in 1945 and Gunter served as editor of that journal from 1950 to 1955.

In 1955, Dr. Gunter accepted the appointment as Director of the then eight-year-old Gulf Coast Research Laboratory in Ocean Springs, Mississippi. That same year he married the former Miss Frances Hudgins of Kosciusko, Mississippi. They produced two sons, Edmund Osbon Gunter, born in 1960, and Harry Allen Gunter, born in 1964. Dr. Gunter doted on these sons and almost always referred to them as his "little boys", I suppose in contradistinction to his older children who would have been pretty well grown up at the time. In his memoirs, Dr. Gunter has referred to his older children as his "brood of little Texans". Dr. Gunter was indulgent of his "little boys'" vitality and encouraged them in some practices that I suppose must have been unsettling to Mrs. Gunter, who usually went along with the program cheerfully enough. One activity that seemed to amuse Dr. Gunter very much involved asking red-haired Harry, the younger boy, to "Climb the walls, Harry; show our visitor how you do it!" At which point Harry would dash across the room, propel himself against the wall and take two or three steps up the vertical wall. This effort would take him along pretty well toward the ceiling, at which point he would somersault and land on the floor with a resounding thump, sometimes on his feet, sometimes not.

Mrs. Frances Gunter is now retired after a distinguished career as an elementary school teacher; Harry is a medical investigator and lives in Purvis, Mississippi, with his family. Edmund has for several years now worked with technical aspects of production with educational television in Mississippi and seems to have retained some of his father's interest in things natural.

Gordon Gunter, during the course of his directorship at the Gulf Coast Research Laboratory, took the place from

a part-time summer school teaching facility to a full-time year-round research facility, and much of the significant early research in the northern Gulf of Mexico took place here under his direct supervision. Dr. Gunter started out with one full-time scientist and two part-time support personnel. At the time of his retirement, GCRL programs were conducted by about 100 senior marine scientists, technical staff, and support personnel. Dr. Gunter was a 50-year member of the American Fisheries Society, a charter member and president of the World Mariculture Society, later named the World Aquaculture Society, and a member and president of the Mississippi Academy of Sciences. His lifetime body of work is represented by over 330 scientific papers and articles, both scholarly and popular. His earlier works regarding the relationships of salinity and temperature of the northern Gulf to marine life have been required university readings to an entire generation of marine biology students (see Selected Bibliography). He was singlehandedly responsible for establishing and developing GCRL's library, which may well be the premier marine library on the Gulf Coast and today bears his name. In the early 1960s, Dr. Gunter developed the concept of *Gulf Research Reports* as a mechanism "... devoted primarily to publication of the data of the Marine Sciences, chiefly of the Gulf of Mexico and adjacent waters."

As early as 1968, Dr. Gunter was working with a handpicked staff of physiologists to formulate an artificial diet for raising shrimp. Even though no particularly high level of technology existed for culturing shrimp at that time, it is apparent that Gunter understood the inevitability of such development, which was, of course a burgeoning industry by the mid-1980s. Gunter always believed that one of the major needs in the north central Gulf of Mexico was a large, long-term effort to discover the full effects of the Mississippi River on the biology of the fisheries resources in the area. "We have learned much but there are still too many things unknown about the River's influence," he said. "This work alone is enough to keep a multi-disciplinary team of workers busy for 20-25 years, and that would be quite an accomplishment." Gunter frequently conjectured as to what the "real natural history" of the Mississippi River would be if the Army Corps of Engineers would stop tinkering with it. Most competent hydrologists concur that without control efforts, the natural tendency would be for the Atchafalaya to "capture" the flow of the Mississippi River. In other words the Mississippi River, instead of flowing past New Orleans, would turn westward and enter the Gulf of Mexico near Morgan City, Louisiana. On one occasion he spent many days at his desk, clucking and scribbling and calling

and harassing various libraries for historical river flow data of the Mississippi River proper as contrasted to flows down the Atchafalaya River. He concluded that the tendency was for the Atchafalaya to grow and the Mississippi to diminish in such a manner that by the year 2038 these two rivers would be of equivalent size.

Gunter's career as a marine biologist and leader in marine research and education spanned more than 60 years. After stepping down as Director of GCRL, he continued his association with the Laboratory as professor of zoology and director emeritus until his retirement from active service to the State of Mississippi in 1979 at the age of 70. "He was one of the pioneers," retired GCRL Director Thomas D. McIlwain, said. McIlwain, now a National Marine Fisheries Service administrator, was a leader in nominating Gunter's name for a National Oceanic and Atmospheric Administration (NOAA) research vessel in recognition of the marine scientist's fisheries work in the Gulf of Mexico. The NOAA ship *Relentless* was moved to the Gulf of Mexico and commissioned as the *Gordon Gunter* on August 28, 1998, with Dr. Gunter in attendance at the ceremonies.

About 1977, I was invited to accompany Dr. Gunter on a trip to Texas and we found ourselves in Goldonna, Louisiana, where he wanted to show me his boyhood home. We spent part of that afternoon wandering about in the old Goldonna Cemetery, where Dr. Gunter would point out where his parents were buried and the markers of cousins, uncles and other kin. On December 19, 1998, Gordon Pennington Gunter joined them, and I will miss him. No more will I have a traveling companion whose standard traveling accouterment consisted of a handgun, an Authorized King James Version of the Bible, and a quart of bourbon.

#### ACKNOWLEDGMENTS

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